AUSTRALIAN MUSEUM MEMOIRS

8

1942 - 45

NAT. MUS., VIC.

SHOUT
SHARE
IT

Australian
Museum

Memoirs

VIII

1942-45

National Museum
of
Victoria

M, SYDNEY

HE SKULL
MUSCLES
Development
gy

D.Sc., M.D.

E TRUSTEES.

tor.

D

THE AUSTRALIAN MUSEUM, SYDNEY

MEMOIR VIII.

THE EVOLUTION OF THE SKULL AND THE CEPHALIC MUSCLES

A Comparative Study of their Development and Adult Morphology

By

H. LEIGHTON KESTEVEN, D.Sc., M.D.

PUBLISHED BY ORDER OF THE TRUSTEES.

A. B. Walkom, D.Sc., Director.

Sydney, 1942-1945.

The following are the dates of publication of the four numbers of this MEMOIR:

Number 1, pages 1–62 and i-iv: 30 June, 1942.
Number 2, pages 63–132: 30 June, 1943.
Number 3, pages 133–268: 19 May, 1944.
Number 4, pages 268–310: 13 June, 1945.

CORRIGENDA.

Page 36, line 3. For *Taeniura lymna* read *Taeniura lymma*.
Page 82, line 10 from bottom. For Coccillans read Coecilians.
Page 187, lines 10 and 15. For Caecilians read Coecilians.
Page 100, line 15. For Bridge . . . (1879) read Bridge . . . 1878.
Page 200, line 26. For Bridge in 1893 read Bridge in 1898.
Page 253, line 4. For Lightoller (1935) read Lightoller (1939).
Page 267, line 18. For spheno-pterygoideus anterior read pterygoideus anterior.

LITERATURE SUPPLEMENT.

Brock, Gwendolen T., 1937.—The Morphology of the Ostrich Chondrocranium. *Proc. Zool. Soc. Lond.*, (B) 107, pp. 225–243.

Fairley, N. H., 1929.—Dentition and Biting Mechanism of Australian Snakes. *Med. Journ. Australia*, March 9, 1929, pp. 313–327.

Futamura, R., 1907.—Beiträge zur vergleichenden Entwicklungsgeschichte der Facialismuskulatur. *Anat. Heft*, 32, pp. 479–575.

Gaupp, E., 1906.—Die Entwickelung des Kopfskelettes. *Hertwig's Handbuch der vergleichenden und experimentalen Entwickelungslehre der Wirbeltiere*, iii, 2 Teil, pp. 573–874.

Goodrich, E. S., 1909.—Vertebrata Craniata: Cyclostomes and Fishes. Lankester (ed.). *A Treatise on Zoology*, part ix. Oxford, 1909.

Lubosch, W., 1933.—Untersuchungen über die Visceralmuskulatur der Sauropsiden. *Morph. Jahrb.*, lxxii, pp. 584–666.

Lightoller, G. H. S., 1939.—Probable Homologues. A Study of the Comparative Anatomy of the Mandibular and Hyoid Arches and their Musculature. Part I. Comparative Myology. *Trans. Zool. Soc. Lond.*, xxiv, pp. 349–426.

Luther.—*Fide* Edgeworth, *Journ. Anat.*, lix, 1925, pp. 225–264.

Norris, H. W., 1908.—The Cranial Nerves of *Amphiuma means*. *Journ. Comp. Neurol.*, xviii, pp. 527–568.

Osawa, G., 1898.—Beiträge zur Anatomie der *Hatteria punctata*. *Archiv. mikr. Anat.*, li, pp. 481–691.

Pollard, H. B., 1892.—On the Anatomy and Phylogenetic Position of *Polypterus*. *Zool. Jahrb.* (*Anat.*), v, pp. 387–428.

Regan, C. Tate, 1923.—The Skeleton of *Lepidosteus*, with remarks on the Origin and Evolution of the lower Neopterygian Fishes. *Proc. Zool. Soc. Lond.*, pp. 445–461.

Sagemehl, M., 1891.—Beiträge zur vergleichenden Anatomie den Fische. IV. Das Cranium Cyprinoiden. *Morph. Jahrb.*, xvii, pp. 489–595.

TAXONOMIC LIST AND INDEX OF THE SPECIES AND GENERA OF WHICH THE MUSCLES HAVE BEEN STUDIED.

- Pisces. Pp. 11–104.
  - Elasmobranchii. Pp. 11–43.
    - Selachii Pp. 11–28.
      - *Acanthias* (*Squalus*) *megalops* Macleay=*Flakeus megalops* (Macleay).
      - *Brachaelurus modesta* Gunther=*Brachaelurus waddi* (Bloch and Schneider).
      - *Carcharinus* sp.
      - *Chiloscyllium punctatum* Muller and Henle.
      - *Mustelus* sp.=*Emissola antarctica* (Gunther).
      - *Orectolobius maculatus* (Bonnaterre).
      - *Pristiophorus cirratus* (Latham).
      - *Sphyrna blochii* Cuvier=*Sphyrna lewini* (Griffith).
    - Heterodontidae. Pp. 28–35.
      - *Heterodontus portusjacksoni* (Meyer).
    - Batoidei. Pp. 36–52.
      - *Dasyatis brevicaudatus* Hutton=*Bathytoshia brevicaudata* (Hutton).
      - *Hypnarce subniger* Dumeril=*Hypnarce monopterygium* (Shaw and Nodder).
      - *Raja australis* Macleay.
      - *Taeniura lymma*=*Taeniura lymnia halgani* (Lesson).
      - *Urolophus testaceus* (Muller and Henle).
    - Chondrostei. Pp. 52–56.
      - *Acipenser* sp.
      - *Polyodon* sp.
      - *Psephurus gladius* Martens.
    - Holocephali. Pp. 56–63.
      - *Callorhynchus antarcticus*=*Callorynchus milii* Bory.
      - *Chimaera ogilbyi* Waite=*Psychichthys ogilbyi* (Waite).
  - Teleostei. Pp. 43–104.
    - Crossopterygii.
      - *Polypterus* sp.
    - Actinopterygii.
      - *Lepisosteus osseus* (Linné).
      - *Lepisosteus platystomus* Rafinesque.
      - *Armia calva* Linné.
    - Acanthopterygii
      - *Anguilla reinhardtii* Steindachner.
      - *Balistapus aculeatus* Linné.
      - *Cantherines ayraudi* Quoy and Gaimard= *Nelusetta vittata* (Richardson).
      - *Cnidoglanis megastomus* Richardson.
      - *Drepane* (*Drepanichthys*) *punctatus* Linné.
      - *Epibulus insidiator* Pallas.
      - *Fistularia petimba* Lacépède.
      - *Girella cuspidator* should be *Girella tricuspidator* Quoy and Gaimard.
      - *Gonorhynchus greyi* Richardson.
      - *Hemirhamphus intermedius* = *Reporhamphus australis* (Steindachner).
      - *Mugil cephalus* Linné=*Mugil dobula* Gunther.
      - *Platycephalus fuscus* Cuvier and Valenciennes= *Planipora fusca* Cuvier and Valenciennes.
      - *Tandanus tandanus* Mitchell.
      - *Zanclistius elevatus* Ramsay and Ogilby.

TAXONOMIC LIST AND INDEX OF THE SPECIES AND GENERA OF WHICH THE MUSCLES HAVE BEEN STUDIED.—*Continued.*

Amphibia. Pp.133–187.	Neoamphibia.	Dipneusti. Pp. 133–144.	*Neoceratodus.* *Leipdosiren.*
	Euamphibia.	Coecilia. Pp. 187–191.	*Herpele.* *Ichthyophis.*
		Urodela. Pp. 155–180.	*Amblystoma* (*Axolotl*) *tigrinum* Green. *Diemyctylus* sp. *Molge* (*Notophthalamus*) sp. *Necturus maculatus* Gray. *Plethodon* sp. *Spelerpes* sp.
		Anura. Pp. 143–154, 180–187.	*Hyla aurea* Lesson. *Hyla caerulea* Gunther. *Lymnodinastes peronii* Bibron. *Lymnodinastes tasmaniensis* Gunther. *Myxophyes fasciolatus* Gunther. *Rana pipens* Shreber.
Reptilia. Pp. 238–269.		Lacertilia. Pp. 238–253.	*Amphibolurus muricatus* Shaw. P. 246. *Anolis carolinensis* Dumeril and Bibron. Pp. 246–7. *Anolis cristatellus* Dumeril and Bibron. *Basiliscus* sp. Pp. 247–8. *Chameleon* sp. Pp. 248–250. *Gymnodactylus* sp. Pp. 250–251. *Lygosoma* sp. P. 251. *Physignathus lesueurii* Gray. Pp. 235–246. *Thecodactylus* sp. Pp. 250–251. *Tiliqua scincoides* Shaw. Pp. 251–2. *Varanus* sp. Pp. 252–3.
		Rhyncocephalia. Pp. 253–255.	*Sphenodon.*
		Crocodilia. Pp. 255–260.	*Alligator* sp. *Crocodilus.*
		Chelonia. Pp. 260–264.	*Chelodina longicollis* Shaw. *Emydura macquarii* Shaw.
		Ophidia. Pp. 264–269.	*Notechis scutatus* Peters. *Python variegatus* Gray. *Pseudechis porphyriacus* Shaw.

NATIONAL MUSEUM OF VICTORIA

24 JU 1942
VICTORIA

THE EVOLUTION OF THE SKULL AND THE CEPHALIC MUSCLES: A COMPARATIVE STUDY OF THEIR DEVELOPMENT AND ADULT MORPHOLOGY.*

By H. LEIGHTON KESTEVEN, D.Sc., M.D.

PART I. THE FISHES.

Preface.
The Muscles of the Elasmobranchs: Introduction; 1. Selachii; 2. *Heterodontus*; 3. Batoidei; 4. Review; 5. Chondrostei; 6. Holocephali.
The Muscles of the Bony Fishes: 1. The Muscles of the Branchial Segments; 2. The Constrictor Muscles of the Hyoid and Mandibular Segments; 3. The Hyoid Muscles other than the Constrictors; 4. The Muscles of the Mandibular Segment other than the Constrictors; 5. The Innervation of the Eye Muscles.
The Skull in the Elasmobranchs.
The Skull in the Bony Fishes: Appendix A. The Lower Jaw in Bony Fishes; Appendix B. The Teeth of Fishes.
The Homologies of certain of the Bones in the Skull of the Bony Fishes.
The Phylogeny of the Fishes.

PREFACE.

This work is the result of half a lifetime devoted to the study of the small portion of comparative anatomy and embryology it deals with. For the most part it records actual personal observation. The deductions relative to homologies and the evolution of the vertebrata which the work contains are those which, from my own observations, appear to me to be the most acceptable. These conclusions are in several important instances at variance with those commonly accepted.

Nowhere are the conclusions in the fields of speculative morphology, homologies and evolution, presented as proven. In no single instance have I felt entitled to write Q.E.D. at the end of any section.

An attempt has been made to describe the cephalic musculature of a representative range of each group of the vertebrates. Only such references to the nervous structures have been made as appeared necessary to a proper understanding of the musculature. It is regretted that it has not been possible to include references to the main arterial and venous trunks in their relation to the muscles. It was very early found that it was impossible to dissect, with any degree of success, the blood-vascular system in specimens which had not been injected. Following on this discovery, it was found impossible to obtain specimens already injected, or sufficiently fresh to inject, in sufficient number to make the study even approximately complete. Whilst one must admit that a knowledge of the relation of the muscles to the main blood vessels is desirable, it is believed, looking back over the work done and the observations made, that the conclusions relative to the homologies and phylogenies of the muscles are based on sufficient evidence to justify them, and that a knowledge of the relation to the pertinent blood vessels would, in all probability, add further evidence in support of those conclusions.

Very naturally the embryological work has been largely confined to the later stages of development, during which the muscles are assuming their adult forms. My observations are largely based on actual dissections or serial sections.

In the sections dealing with the cranial structures, descriptions and illustrations of representative forms are given and then the serial homologies of certain of the bones are discussed. It may be accepted that throughout the work all those bones which have been named alike and not been discussed are believed to be homologous, wherever found. These are, of course, those bones about whose homology there is at present complete agreement. Discussions only centre around certain of those about whose homology there is a diversity of opinion.

---

* The complete Memoir, of which this is the first part, contains the following sections: I. The Fishes; II. The Amphibia; III. The Sauria; IV. The Theria.

The work was begun in almost complete ignorance of myology and without any preconceptions, either definite or indefinite, as to what I was going to learn. I had been interested in the cephalic muscles of *Callorhynchus antarcticus* (Kesteven, 1933) and was rather dissatisfied with my description thereof. Although a few bony fishes had been dissected in an attempt to understand the musculature of that fish, it was felt that the attempt had been a failure. This caused me to dissect a number of Selachians, and in the course of this work I conceived the idea that since the mandibular and hyoid arches were probably modified branchial arches, their musculature must be modified branchial musculature. At this stage the work took its first form: the objective was to test this theory.

In this part of the work it was believed that success in the interpretation of the muscles could be expected only if due weight were given to the probable mechanical factors operative during the change in form and function of the arches. These mechanical factors were deemed to have been, in all probability, more potent than mere spatial relations. The most important result of this investigation, in its bearing on the outlook over the subsequent fields of investigation, was the conclusion that the muscles of the mandibular and hyoid segments could only be interpreted in terms of the branchial on the assumption that not all the branchial muscles had been retained, some had been aborted.[1]

The reasons for this conclusion will be found in the text, but, apart from the circumstantial evidence specifically applicable to each case, there is collateral evidence of a quite general kind in support. The wide variation observable in the muscles of the vertebrates justifies the belief that "muscles", wherever they are found, may be regarded as contractile tissue fashioned to fit the mechanical needs and spatial relations of the structures they are called upon to move. Therefore every muscle must be regarded as a particular exemplar of this generality; in point of general significance none is unique. Therefore the mere existence of those instances of adaptation to peculiarities which are to be found in small groups and single species only, illustrates the fact that muscles are only developed in association with a mechanical need, and this implies and accepts the converse as equally true—muscles are not developed in the absence of the mechanical need. One outstanding and unchallengeable illustration of the concept alone will be quoted. The branchial constrictors of the Selachii have completely gone from the higher Vertebrata with the loss of the interbranchial septa.

The importance of this concept is that it has constantly determined the mental approach to the problems arising throughout the whole of the work subsequent to that on the Selachii. The Selachii were regarded as the most primitive vertebrates, and it was anticipated that all the muscles of the higher vertebrates would prove to have been derived from some of those of these primitive fishes, but it was not anticipated that all the muscles of the fishes would prove to have been retained throughout the series.

Lightoller has claimed, for the adoption of a belief that "all the groups of muscles found in the Selachian hyoid and mandibular regions are represented in each of the higher orders of Vertebrates", that "it corrals imaginative theory, and is less open to objection than the inconsequent dropping of an inconvenient muscle sheet". (Lightoller, 1939, p. 350.)

Dr. Lightoller and the writer have worked alongside of one another almost, and have discussed the work as it progressed. This is one of the questions on which we have agreed to differ.

My colleague's position seems untenable for the following reasons. It is demonstrable that single muscles and whole sheets are aborted. Quite apart from the phylogenetic example quoted above, the absorption of single muscles and groups of muscles may actually be observed during the metamorphosis of the amphibians. If it is demonstrable that muscle sheets, groups and/or individuals have been aborted in certain segments, then it seems that one is not justified in denying the possibility of abortion in all segments.

Undoubtedly my decision of the last paragraph has been influenced by the personal factor, and that factor appears even more strongly in the following. Lightoller dismisses the branchial interarcual and adductor muscles with the remarks (p. 355) "These, embryologically (Edgeworth), are derived from the constrictor sheet, and are no longer recognisable in the hyoid arch. It is thought that their fate must be that of the parent constrictor, so no special description of them has been given." It is quite impossible to keep the personal factor out of inquiries of this kind. In the absence of mathematical methods of testing the accuracy of one's conclusions there is left only the expression of one's opinion, and to deny the existence of the personal factor, even tacitly by ignoring its presence, would be to adopt a quite unjustifiable dogmatic attitude. In this case it appears that Lightoller has, at the outset, departed from his intention to find representatives of all the groups by discarding a quite important group before he begins. To the writer the branchial adductors stand as the first stage in the evolution of the muscles of mastication.

---

[1] I plead guilty to a belief which appears to be old fashioned and to be becoming discredited. I am unable to believe that the growing organism does not respond to its environment by adaptation thereto, nor can I think that this response is without effect upon the germ cells. I know of no evidence, experimental or otherwise, which should destroy a belief that the germ cell will react to changes in its environment. The environment of the germ cell is the body fluid in which it grows. The content of this fluid will surely vary with the size and degree of activity of every part of the body. Here is not the place to elaborate this belief further, but this short statement of the thought processes behind the attitude adopted in the above paragraph seemed called for.

Finally, it appears to the writer unwise to "postulate conditions" into which the facts are to be fitted. That this was done by Lightoller seems evident from his statement relative to his third clause, quoted above, that it had made his "task more difficult and, at times, its wisdom seems questionable".

The writer's view may be stated as follows: The myotome alone is unquestionably persistent, and only those derivatives of it which investigation seems to demonstrate so may be regarded as having persisted throughout the groups and orders of the vertebrata.

The weight given to the influence of mechanical factors in the evolution of the muscles has been such that always it has been assumed that these factors have persisted with the muscle, or that there has been a gradual change in them which has permitted or brought about the changed relations of the persistent muscles.

During these ten years of study of comparative myology of the head and neck, the ease with which it has been possible to recognize so many of the muscles of the last class in the next which fell for study has been recurrently surprising. Infinitely more difficulty in recognizing homologous muscles was anticipated, and the rarity of difficult and insoluble puzzles was very unexpected.

It is realized that this absence of difficulty may have been more apparent than real, that puzzles have not presented difficulties because wrong solutions have been accepted. It is believed that this will prove to have been the case in very few instances and that in the main the conclusions arrived at are correct.

One outstanding generality seems to emerge from this simplicity of the problem, namely, that the association of nerve and muscle in the neuromuscular unit must have been very firmly established very early in the process of differentiation of the vertebrate stock, because this constancy of neuromuscular association has been so successfully used throughout the work as the initial guide to the identification of the muscles.

It is a fact that, with very few exceptions, muscles of any given segment are, without doubt, innervated by the nerve of the same segment. The exceptions to this rule are for the most part questionable. The statements that they *are* exceptions are based upon dissections, and are inadequately or not at all supported by experimental evidence and/or embryological proof. In almost every instance, moreover, such statements conflict with those of other investigators. The rarity of these cases is itself a reason for doubting the verity of the exceptional association said to be present.

The statement that a muscle is innervated by a nerve other than that of the segment to which the myotome belonged, e.g., that a muscle derived from the mandibular myotome is innervated by the seventh nerve, implies a great deal more than the mere anatomical association. It is a statement which implies the breakdown of the definite forces, whatever they may be, which direct the progress of ordered ontogenetic growth and development.

We are faced, it appears to me, with two, and only two, possibilities in this connection; we must assume that there are physico-chemical forces directing the processes of growth, or else we must assume that there are no directors whatever. The facts of ordered growth are, in themselves, the complete refutation of the second.

The first assumption, however, at once forces upon us the recognition that the governance of ordered growth is under the direction of both stimulating and inhibiting forces.*

---

* It would not add to the exactness of this discussion to attempt to employ any of the recognized designations. We might, for instance, refer to the responses as tropisms, or positive and negative morphogenetic substances or centres, or as excitors or inhibitors or evocators. Until we know a great deal more about these things they are little more than useful terms defining the method of approach to the general problem, and implying a belief in the existence of a directing force.

Since the muscles come to assume certain constant and definite relations, in each species, to contiguous structures, we must assume that something has directed development to this end, and further, that something has prevented them from acquiring other relations. Similarly, both positive and negative forces must have been effective in determining the association of nerve and muscle, and this will have been so whether the theory of His be correct, or that of Hensen; whether the nerves have grown peripherally or centripetally.

The experimental work of Lehmann, Detwiler (Detwiler, 1936, pp. 147–150) and others has provided the proof of the existence of the positive force determining the direction of nerve growth, and (accepting the His theory) that it resides in the mesoderm of the segment for the segmental nerve, and in the limb bud for the brachial plexus. It has been further shown that, if the mesoderm be completely excised, the development of the segmental ganglion and of the peripheral fibres is more or less completely inhibited.

The negative controlling force has not as yet been located. It is here suggested that this may reside in the growing nerves themselves and be exercised upon contiguous nerves, so that they exercise a mutual repulsion upon one another. This would explain why segmental nerves are confined to girdle areas of the body and only overlap to a small extent. This idea may be given better definition by suggesting that a morphogenetic hormone is formed in the neighbourhood of the growing nerve, which, diffusing into the surrounding tissues, inhibits the growth of other nerves in the regions of its greatest concentration.

This suggestion might be tested by the early excision of half of the neural crest in a single segment. If the suggestion be the correct explanation, then one would expect the segmental nerves on both sides of the gap to supply at least sensory nerves to the area deprived of its own nerve.

However, whatever be the correct explanation, it seems certain that the orderly growth of nerves must be under the direction of positive and negative forces. Therefore heterogeneous innervation* can only have resulted from the breakdown of these forces.

If the reality of those forces be admitted, it becomes worth while considering just what their "breakdown" must imply. The experimental work previously referred to demonstrated that nerve-muscle attractions were not specific, that mesoderm, or more specifically muscle plate, from any segment was capable of receiving nerve tissue from any other segment into which it was transplanted in place of the muscle plate thereof, and that the limb bud was capable of exciting the development of the nerves from other segments than the normal, if transplanted, so that its plexus was derived from segments other than the normal.

Therefore, it might seem that any muscle might exercise an attracting influence on any nerve. Whilst the muscle is in the normal situation, however, it will be supplied by its own proper nerve. Before we can admit the occurrence of heterogeneous innervation we must postulate the failure of the proper nerve to grow, although, since it attracts another nerve, *ex hypothesi*, the muscle was possessed of the power to have attracted its own proper nerve.

If we assume that the change over was gradual and not effected at a single step, then we assume something for which there is no evidence in support from experimental work: we assume that the invading nerve had grown away from its own proper stimulating directive force and against the inhibitory force which seems to reside in any area supplied by its own proper nerve.

Finally, although experimental work appears to have demonstrated that the stimulating directive force is not specific, we are called upon to postulate its failure to stimulate one nerve whilst retaining the power to stimulate another to growth, that is to say, we have to postulate specificity in one small isolated phenomenon, as well as postulating the failure of an inhibiting force which also is probably not specific.

Whilst it is recognized that these thoughts relative to the control of the development of the nerve-muscle units are very largely pure speculation, it is claimed that they do present the probabilities, and the conclusion they force upon one is that all claims for heterogeneous innervation must be regarded with grave suspicion.

The evidence for and against the specific examples of apparently heterogeneous innervation will be found in its appropriate place in the text.

Scattered throughout the work will be found specific acknowledgments and thanks for assistance from colleagues and friends, too numerous to detail here, but I should like in this place to express my thanks and acknowledge my debt to Dr. C. Anderson, formerly Director of the Australian Museum, Professor A. N. Burkitt of Sydney University, and Dr. Lightoller.

---

* This term is used to indicate the innervation of structures derived from one segment by a nerve from another segment.

Throughout the progress of the work Dr. Anderson placed the resources of the Museum at my disposal, and to his kindly interest in this way I owe a multitude of interesting specimens.

To Professor Burkitt's active interest in my work, I owe inspiration and direction in many ways. I am also indebted to him for assistance which I have constantly had from the Department of Anatomy, which he directs.

Dr. Lightoller's assistance has taken the form of keen criticism, which his own work in muscle homologies and consequent understanding of the problems has always justified. The fact that we have not always been able to agree has been, in those instances, a spur, for the resultant discussions have indicated wherein my case was weak, leading, in some instances, to modification of my views and, in others, to the strengthening of my argument by further investigation.

Finally I should like to acknowledge my indebtedness to the Executive of the Commonwealth Council for Scientific and Industrial Research for grants which have purchased material and instruments for my use.

Post Scriptum.—After this first part of my work was completed, Edgeworth's exceedingly fine book on the Cranial Muscles of the Vertebrates (1935) reached me. Brief comment on certain points of agreement and of difference between us appears desirable.

Edgeworth states (p. 25): "Ichthyopsida and Amphibia can be divided into two groups with reference to the developmental phenomena in the masticatory muscle plate . . . The first comprises Dipnoi, Holocephali and Amphibian larvae", and presumably adult Amphibia. The second group comprises Plagiostomi and Teleostomi. The former are said to exhibit a "primary" mode of development of the masticatory muscle plate, the latter group a "secondary" mode. He comes to the conclusion that on account of this difference in the mode of their development the Mm. adductores mandibulae of the former are not homologous with those of the latter group, and therefore designates the adductors in the first group "levatores mandibulae". Edgeworth further stresses the fact that the secondary mode of development, that of the Plagiostomes and Bony fishes, is found in the Sauropsida, whilst the primary mode is present in the Mammals. This complete discontinuity he explains by assuming that the secondary condition has been separately acquired.

Edgeworth appears to be of the opinion that early embryonic conditions must represent and be derived directly from ancestral features; or is it that his conviction that the Dipnoi are the most primitive of living forms leads him to adopt the above view?

There is so much clear and conclusive evidence that no embryo may be accepted as representing an adult ancestor that the first position appears to the writer as untenable. The second position, if that be the correct interpretation of his attitude, will have been the result of the personal factor in the equation, and must be recognized as entirely justifiable.

Obtruding that same personal factor, I have always regarded the appeal to coincidences and fortuitous happenings as a weakness in attempts to explain phenomena of development and adult anatomy.

It appears to me that the most we are entitled to assert is that the mesodermal segments and their derived neuro-muscular units *as a whole* are homologous. Beyond that we enter the realm of speculation. This is not to be interpreted as meaning that we are not justified in attempting to derive this muscle from that or the other, and to that extent regarding them as homologous. I would derive the M. depressor mandibulae of the Amphibia from portion of the primitive hyoid constrictor sheet of muscle fasciculi of the Elasmobranchs, but with quite different origin and insertion it hardly seems reasonable to claim complete homology for the two muscles.

With so wide a variation in the adult structures, and so much evidence of the variability of the earliest embryonic features—an outstanding example is the varied development of the premandibular somite—it does not appear that one is on safe ground when basing argument for, or against, homology on the early condition of the muscle plate.

In the present instance we do not know, and are likely to remain unable to know, whether the missing dorsal muscle is incorporated into the Mm. "levatores mandibulae", or whether the mother cells of these muscles have simply dropped from the ontogeny altogether.

Whilst it were very largely in accord with my own interpretation of the modification of an originally continuous primitive constrictor sheet, to regard the continuous, uninterrupted cranio-meckelian maxillary muscle plate as the more primitive condition, I am unable, in view of the evidence, as I see it, to adopt this view. To my mind the simpler explanation and the one that avoids the appeal to coincidence is that the muscles derived from the dorsal part of the sheet, the constrictor dorsalis portion, have been so completely lost or incorporated in the lower muscles by the members of the first group, and by the Mammalia, that there is no division of the embryonic sheet.

In support of this view, I would point out that the Holocephali so closely resemble the Plagiostomes in the great majority of their cephalic characters, that one is obliged to regard them all as Elasmobranchs. The greater geological antiquity of the Plagiostomes leads me to expect them to present the most primitive conditions. I have regarded the subdivision of the mandibular muscle sheet into dorsal constrictor-levator, middle adductor and ventral constrictor components as being the modifications of a branchial sheet, brought about by the modifications of the related mandibular arch. The absence of the dorsal component, observed in the Dipnoi etc., I would regard as the suppression of these muscles, which might be expected to follow naturally upon the firm fixation of the maxillary half arch.

The same line of thought leads me to regard the selachian evidence relative to the ocular muscles, as indicating that they were originally derived from the premandibular, mandibular and hyoid muscle plates, and to regard the VIth nerve as part of the VIIth and the IVth as part of the Vth. To me, the varied mode of origin of these six muscles and of the premandibular somite appears as the result of the pressure or other influence of the varying juxtaposed structures.

It is pleasing, however, to note that Edgeworth regards the Dipnoi and the Amphibia as being derived from a primitive Dipnoan stock. I arranged the evidence in support of this view some years ago (1931), and was closely followed by Kerr (1932) in the same vein. It is also pleasing to me to find that the similarities to one another, presented by certain of the cranial features in development and adult anatomy of the Holocephali, Dipnoans and Amphibians, have appealed to Edgeworth as being fundamental.

After carefully studying Edgeworth's book I still feel that my diagram II, schematically portraying the phylogenetic relationships of the Anamniota, most nearly represents the correct interpretation of the facts at present available.

THE MUSCLES OF THE ELASMOBRANCHS.

Introduction.

Profound modifications of both the skeletal structures and their activating muscular mechanisms are to be observed in the heads of recent fishes. Muscle entities seem to develop, disappear, and reappear in bewildering variety with each change in underlying skeletal frame, or overlying dermal condition.

The head develops a rostrum and at once levator and depressor rostri appear ; let the dermis be rigid and there are no facial muscles, but if the dermis be soft then, as in the Holocephali, a complete set of superficial facial muscles is at once developed ; given a modification of the attachment of the superior labial bones, as in *Drepane* or *Epibulus*, so that the upper lip becomes protrusible, the requisite modification of the muscles of mastication surely follows. Clearly the homologue of the levator rostri should not be sought in a fish which has no rostrum, nor that of the protractor labii superioris in a fish which has rigidly attached labial bones.

These last two instances exemplify extreme limits of the problem of the evolution of the cephalic musculature of the vertebrata. They are special developments in harmony with special skeletal developments, and are not to be found in the absence of those skeletal modifications. But whence came they ? Not from nothingness : they are to be regarded as derivatives of some portion of that early muscle plate which gives rise to the other more normal muscle entities present.

It appears as though modification of the muscular system and its evolution are essentially dependent on, or conditioned by, modification and changes in the skeletal system. There is, moreover, a marked difference of attitude to be maintained in the study of cranial evolution on the one hand and of phylogenetic myogeny on the other. In the former case experience points to the expectation of reduction in the number of the component elements, either by more or less complete fusion or deletion of the elements, and an absence of the introduction of new elements. In the latter case one must be prepared, not only for fusions and deletions, but also, and increasingly in the higher forms, for the introduction of completely new entities.

Thus a study of the evolution of the musculature of the vertebrate head may prove an attempt to understand the origin and modification of the various muscles rather than a search for homologies.

As an introduction to such a study, this first section is devoted to an attempt to understand the metameric serial homologies of the muscles of the heads of the various fishes. It would seem that, omitting the epibranchial and the hypobranchial spinal muscles, the muscles of the fish's head are modified forms of the original metameric repetition of similar muscles related to the visceral arches. If these original elements can be identified in their modified forms, such identification should assist us in understanding the further modifications in the higher vertebrata.

It is probable that the primitive vertebrate was provided with a terminal, or subterminal, mouth, behind which ranged seven visceral arches. It is further probable that a myotome, or muscle sheet, was present in front of each arch and behind the branchial cleft, that is to say, in the anterior portion of the thickness of each interbranchial wall, and in front of the first arch around the mouth opening. The muscles related to these arches were probably constrictors only, in the most primitive condition, the resilience of the unjointed arches being relied upon to effect a return after constriction (Fig. 1, A).

The accumulated evidence on the form of the visceral arches indicates that each was very early segmented into four pieces on each side, united below by a median piece. There may have been five pieces in each side and the ventral pieces became fused in pairs.

Clearly unless the joints of the arch bent in opposite directions, constriction would have been productive of dorsi-ventral or lateral flattening, or would have displaced the apex of the compressed arch forwards or backwards. The mechanical disability in the way of compact constriction of the throat and mouth could only be overcome by development of these flexions observed in the arches available for study. It is therefore reasonable to believe that the " ≥ " shape of these arches is a very ancient feature. As generic terms for the four segments will prove convenient, pharyngo-, epi-, cerato- and hypo-" arcual " are suggested.

There was no " face ", and, of course, there were no facial muscles in the primitive prognathostomatous vertebrate.

It appears that early modification of the musculature resulted in the attachment of deeper parts of the circular sheet to the jointed arch, and there resulted those muscles which we designate levatores arcuum branchialium, obliqui dorsales, adductores arcuum branchialium and obliqui ventrales (Fig. 1, B).

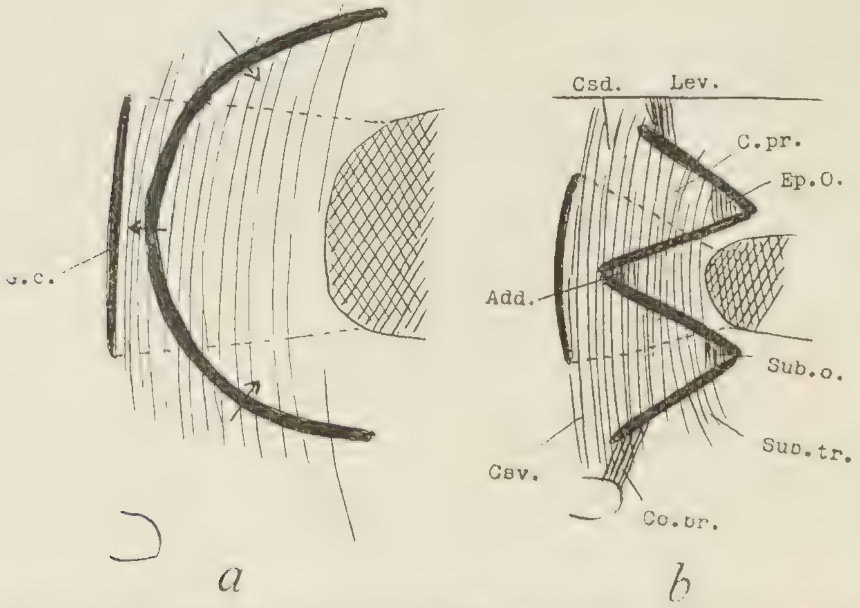


Fig. 1.—A. An hypothetical branchial arch, with its continuous constrictor sheet of muscle and unjointed cartilaginous arch.

B. Scheme of the jointed arch and modified muscles derived from Figure 1A. In both drawings the atrio-pharynx has been indicated by cross-hatching. Add., adductor arcuum. C.pr., deep constrictor. Co.br., coraco-branchialis. Csd., superficial dorsal constrictor. Ep.o., oblique epi-arcual. G.c., gill cleft. Lev., levator arcuum. Sub.o., subarcual oblique. Sub.tr., transverse subarcual.

The effect of this more perfect musculature was to approximate the bisected dorsal and ventral halves of the arches more efficiently, bringing about the actual contact of their fore ends. These fore ends of the folded arches, it will be remembered, are the upper and lower ends respectively of the middle segments. The contact of the fore ends of the front arch would have surely been early availed of as a means to prehension of food. I have elsewhere designated this hypothetical stage in the evolution of the maxillo-mandibular arch, "neognathostomatous". The first arch was assumed to have functioned as a jaw, but was not deemed to have been modified to any degree and was assumed to be slung to the cranium and to its fellows much as the other arches are now.

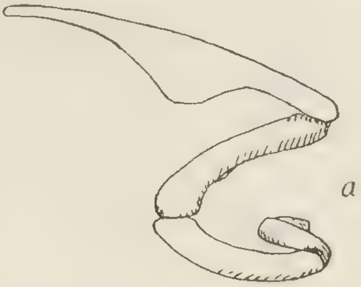
Further modification is regarded as having resulted in the fixation of the first "epiarcual" and it became the palatoquadrate. The first cerato-arcual increased in size and became Meckel's cartilage. The joint between these two became more perfect and stronger. The first pharyngo- and hypo-arcuals became reduced and perhaps persisted as the labial cartilages. Finally, there was increased complexity and efficiency of the muscles related to this first arch and there resulted the perfected jaws.

Along with these changes, and perhaps conditioned by size and backward growth of the upper and lower jaws, there was a modification of the hyoid arch, whose upper element was either impressed as a suspensorium for the first, as in the generality of fishes, or much reduced in size, as in Holocephali, Dipnoi and higher vertebrates generally.

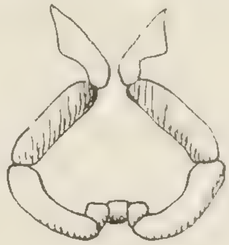
A primitive branchial arch is depicted in Figures 2 and 3, seen from the side and from in front. These drawings also represent conditions present in almost any Elasmobranch. They serve to illustrate the fact that the cerato-branchial cartilages are very closely approximated to one another in the midline, whilst the epibranchial cartilages are nearly as closely related superiorly. There is here nothing to indicate the impossibility of the two most anterior pairs of elements becoming united at the midline above, to form the palatoquadrate arch, just as Meckel's cartilages and the other arches are joined together below.

The remarkable uniformity in the general plan and arrangement of the branchial arches throughout the fishes justifies the conclusion that they are but little modified from the primitive jointed type from which all are evolved. If this be so, one may also assume that their musculature will have undergone relatively little modification.

Since, however, there is variation in the number and arrangement of the branchial muscles in the various fishes, no one of them may be justly accepted as typical of the primitive condition. On the other hand, one may, with tolerable confidence, reconstruct that typical arrangement by making a "composite" picture which shall include all those muscles which commonly occur in all or in the majority of the known forms in each class, omitting muscles which are present only exceptionally and in single classes only. Such a composite picture is presented alongside a schematic presentation of the primitive unjointed arch and its simple muscle sheet, in Figure 1, B.



2



3

Fig. 2.—The jointed branchial arch viewed from the side. A., anterior end.
Fig. 3.—The same, viewed from in front.

In this composite arch the following muscles may be recognized :

Superficial constrictors	dorsal (csd.) ventral (csv.)
Deep constrictor	constrictor profundus (C.pr.)
Levator	levatores arcuum branchialium (lev.)
Epibranchial spinal	passing from one branchial arch to another (d.i.) (not shown)
Adductors	dorsal (epiarcualia obliqui· (ep.o.) middle (adductores arcuum branchialium) (add.) ventral (subarculia obliqui) (sub.o.)
Ventral interarcual	subarcuales recti, passing from one arch to the other (v.i.) (not shown)
Depressor	coraco-branchiales (co.br.)

The nomenclature of Marion, Vetter and Tiesing has been in part adopted. The departures are in the partial acceptance of Edgeworth's nomenclature for the specialized ventral muscles and its extension to the similar dorsal muscles. Edgeworth recognizes subarcualia transversi, obliqui and recti. Of these the first two might be described as *intraarcualia* since they extend from one segment of an arch to another segment of the same arch or to its fellow of the opposite side. This is not entirely true, for the obliqui do in some cases gain attachments to two different arches, but even in these cases the muscle acts essentially as a flexor of the joint it crosses. The recti, on the other hand, are essentially *interarcualia*, for they extend from one arch to another and act to bring these arches together. I would therefore classify these as "interarcual" muscles whilst retaining Edgeworth's specific designation "sub-arcualia recti".

On the other hand, I have applied a modification of his terminology to the essentially similar dorsal intraarcual muscles which, in the past, have been designated "lateral series of dorsal interarcual muscles". These I designate epiarcualia obliqui, but classify them functionally as dorsal adductors.

The dorsal interarcual muscles ("median series of dorsal interarcual muscles") I designate "epibranchial spinal" muscles to convey their origin from spinal myomeres.

It is, of course, always regrettable to add to synonymy, but it appeared essential to obtain a set of designations that was completely free from ambiguity, and in which each term was sufficiently self-explanatory to give rise at once to a mental concept of the situation of the muscle named.

The table which appears above is not only a list, it is also a classification, and it is well worthy of note that all of these muscles, excepting only the levators and depressors, are constrictors of the atriopharynx. In the absence of the levators in such a form as *Heterodontus*, it is found that there is dorsally a deep portion of the interbranchial muscle which is capable of acting as a levator and, further, that in many of the fishes there is a very similar portion of the interbranchial muscle ventrally which is capable of depressing the lower half of the arch and acting as a dilator of the arch and pharynx. That a portion of the deep constrictor should thus easily be modified to act as a dilator is significantly interesting.

We may also here draw attention to the fact that, according to the view adopted in this work, the superficial constrictors and the deep constrictors are to be regarded as but slightly modified primitive muscles, whilst the adductors are specialized developments from the deepest layers of the primitive sheet.

It has been demonstrated by a number of observers, but particularly and with especial clarity by Edgeworth, that the muscles related to the maxillo-mandibular arch are developed from a single "mandibular myotome" and are innervated by the fifth nerve, that the muscles of the hyoid arch are developed from a single "hyoid myotome" and are innervated by the seventh nerve, and that the muscles of each branchial arch are developed from the corresponding "branchial" muscle plate and innervated by a corresponding segmental branch of the ninth and tenth nerves.

A slight discordance is produced by the innervation of the coraco-branchiales muscles in the Plagiostomi, which are innervated by the spino-occipital plexus; there is also further discordance in the innervation of branchial levators and superficial dorsal constrictors by spinal nerves. The epibranchial spinal muscles are innervated by the spinal nerves of the myomeres from which they are developed.

Since the coraco-branchialis muscles are developed from the fused ventral ends of all the branchial muscle plates (Edgeworth, 1926) it was to have been expected that they would be innervated by branches from the proper branchial nerves. Apparently their innervation is a secondary modification. The trapezius, or, preferably, cucullaris, developed from the upper ends of all five branchial muscle plates in *Scyllium*, is innervated by the vagus nerve only.

I have deduced from purely morphological evidence that the primitive musculature was a simple constrictor sheet. It is worthy of note that there is embryological evidence in support of this conclusion.

If this is the fact, and in each branchial wall there has been developed from a simple constrictor muscle sheet the series of muscles illustrated diagrammatically above, we have a fundamental illustration of the truth of an earlier contention—that in the study of the evolution of the cephalic musculature we search for derivatives rather than serial homologues.

The whole of the complicated musculature of the Elasmobranch branchial wall is the homologue of a primitive constrictor sheet and we are irresistibly led to the same conclusion in the case of the muscles of the maxillo-mandibular and hyoid arches; but further than that, if those have evolved from arches similar to the branchial and have passed through similar stages of evolution, it should be possible to recognize in their musculature some trace of that evolution. In short, if in the past the musculature of all the seven arches was the same, it should be possible still to recognize the serial homologues in the modified arches.

There is little doubt that the Elasmobranchs are the most primitive vertebrata available for study, and one naturally turns to the more primitive first in such a problem as the present.

Accepted classification of the Elasmobranchs recognizes two orders, the Plagiostomi and the Holocephali, with two sub-orders of the former, the Selachii, containing the sharks, and the Batoidei, containing the rays.

To these I would add, with ordinal value, three families of the Chondrostei, namely the Chondrostidae, Polyodontidae, and Acipenseridae. The remaining families of the Chondrostei (Bridge, 1904) I would assign to the Osteolepida. A study of their visceral musculature confirms a previous opinion that the above acipenserid fishes are more closely related to the cartilaginous than they are to the bony fishes (Kesteven, 1931).

It has also been found that, whilst there are very definite features in the musculature of the sharks and rays in support of the sub-ordinal division of the Plagiostomi, there are just as definite characteristics in the musculature of *Heterodontus* to justify it being placed in a third sub-order. It appears probable that the Notidanidae and the Cochliodontidae should be placed with the Heterodontidae in this sub-order.

There are therefore five types of elasmobranch cephalic musculature to be described: Selachian, Heterodont, Batoid, Holocephalan and Acipenserid.

1. The Selachii.

In the study of the selachian cephalic musculature I have been enabled to dissect the following material. *Mustelus antarcticus* Günther (ten specimens), *Brachaelurus modestus* Günther (three specimens), and one specimen each of *Orectolobus maculatus* Bonaterre, *Squalus* (*Acanthias*) *megalops* Macleay, *Sphyrna Blochii* Cuv., *Pristiophorus cirratus* Müller and Henle, *Chiloscyllium punctatum* Müller and Henle. This last was obtained prior to the specimens of *Brachaelurus*; their dissection proved the two to be so completely similar that the dissection notes on *Chiloscyllium* have been used, in fact they were found to describe the *Brachaelurus*.

In addition to these, Dr. Lightoller has kindly demonstrated to me his dissections of *Mustelus*, *Orectolobus* and *Carcharhinus*, and I have gratefully to acknowledge his kindness.

For the School Sharks, *Mustelus*, the Wobbegong, *Orectolobus*, and the little Rock Shark, *Brachaelurus*, I have to thank various of my fishing friends. These specimens reached me in the fresh state. For the rest of the specimens I have to thank the Trustees of the Australian Museum and Mr. G. P. Whitley.

Only in the hyoid and mandibular segments was it found desirable to present detailed descriptions of the various muscles in each species. The branchial musculature proved so essentially similar throughout the series that it has been described in general terms.

THE SELACHII.

——		Branchial Segments.	Hyoid Segments.	Mandibular Segment.
Superficial Constrictors.	Dorsal ..	Csd.3–6	Csd.2	Absent
	Ventral ..	Csv.3–6	Csv.2	Csv.1
Deep Constrictors.	Dorsal ..	Cp.3–6	Cp.2	Cd.1
	Ventral ..	Absent	Interhyoideus	Absent
Levators		Lev.3–6	Lev.2	Lev.max.sup.
Epibranchial Spinal muscles		Ep.br.3–6	Absent	Absent
Adductor Muscles.	Dorsal ..	Ep.3–6	Absent	Pterygoideus Lev.lab.sup. (Marion) Add. (Vetter)
	Middle ..	Add.arc.br.	Absent	Quadrato-mandibularis
	Ventral ..	Absent	Absent	Absent
Depressors		Coraco-branchialis	Co.hyoideus	Absent

Hypobranchial spinal muscles. Coraco-mandibularis and coraco-branchialis communis.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Constrictors.

A. Dorsal. Each of the dorsal constrictors presents two portions which, following Lightoller,* I will designate partes inscriptionalis and arcuata. It should be clearly grasped at the outset that each of the constrictor sheets, both superficial and deep, is placed behind its respective gill pouch, but in front of the cartilaginous support of the septum of which it forms the muscular component. This fact is likely to be overlooked by reason of the caudad growth superficially of the septa, causing the posterior portion of each septum to act as the lateral wall of the pouch behind, and, in this portion, not limiting the pouch in front of it. This is liable to lead one to regard the constrictor sheets as being placed in front of their respective pouches.

---

* Lightoller (p. 352) regards the deep constrictor as portion of the superficial, and designates it "pars branchialis". I have followed earlier workers in designating this part of the perfectly continuous branchial sheet the "deep constrictor", because in the hyoid segment throughout the whole of the vertebrata this part of the sheet is deep to the rest; even in the branchial segments the designation is justified by the fact that this part of the sheet is deeply placed, and the other two parts superficially placed.

That portion of the dorsal superficial constrictor which lies superficially, and lateral to the pouch behind, constitutes the pars arcuata; the portion more deeply placed is the pars inscriptionalis. These dorsal constrictors take origin from the aponeurotic investment of the trunk muscles, fascia dorsalis. Each pars arcuata has an origin in common with the pars inscriptionalis of the muscle behind it. From their origin the direction of the fasciculi is ventrad with a convexity laterad. At the superior fornix of the gill pouch the pars arcuata of the one passes superficially, whilst the pars inscriptionalis of the other passes more deeply. At the line of the divergence of these fibres there is either the dorsal extrabranchial cartilage or simply a tendinous interruption.

These dorsal superficial constrictors may pass uninterruptedly ventrad into the corresponding ventral constrictors, or the continuity of the fasciculi may be interrupted by the insertion of more or fewer of their number into a prominent mid-lateral gill-ray, and/or a mid-lateral tendinous interruption which may or may not be confined to the pars inscriptionalis.

B. Ventral.—The four ventral superficial branchial constrictors present partes arcuata and inscriptionalis which correspond to the portions of the respective dorsal constrictors, and in most cases are simply ventral continuations thereof. The insertion of these is: (1) superficially, into the ventral deep fascia on either side of the hypobranchial spinal muscles, and (2) into deeper structures which may be (*a*) the ventral extrabranchial cartilages, which in turn are bound to the ventral surface of the gill arch by fibrous membranes, or (*b*) simply such fibrous membranes without the cartilage. It is, of course, the pars arcuata which is inserted superficially and the pars inscriptionalis which is inserted the more deeply.

THE DEEP CONSTRICTORS.

A. Dorsal.—There are four interbranchial muscles. These are essentially similar to the partes inscriptionalis of the superficial sheet. Not only is this so but, in many examples, it is quite impossible to decide definitely where the one begins and the other ends. The deep portion of the superficial constrictor lies anterior to and in contact with the outer ends of the gill rays, the deep constrictor lies against the inner ends of the same rays. These interbranchial muscles take origin above from the extrabranchial cartilage which at its deep, inner, end is firmly bound to the aponeurosis of the trunk muscles, or they take origin from the fascia dorsalis direct. They are inserted below either into the ventral extrabranchial cartilage or, without its intervention, into the ventral end of the arch. These deep constrictor sheets may or may not be interrupted by the insertion of more or fewer of the fasciculi into one or more of the gill rays. In none of the examples dissected was there found any portion of the interbranchial muscle passing direct to either the epibranchial cartilage from above or the cerato-branchial from below as was found in *Heterodontus*.

B. Ventral.—No complete subarcualia transversi were observed in any of the selachians dissected. On the other hand, I have been able to confirm Marion's observation that some of the fibres both of the pars inscriptionalis and of the deep constrictor in *Squalus* (*Acanthias*), as also in *Mustelus*, find an insertion into the deep fascia of the coraco-mandibularis muscle.

THE BRANCHIAL LEVATOR MUSCLES.

The branchial levator sheet was first described by Lightoller. I have been able to confirm his observations upon *Mustelus* and *Orectolobus*, and have found the same sheet in *Brachaelurus*, *Sphyrna*, *Pristiophorus* and *Chiloscyllium*. In *Squalus* (*Acanthias*) also, the levator sheet is present but so very fine are the several muscles that, had one not been searching for them, it is doubtful whether they would have been observed. *Orectolobus* and *Brachaelurus* are closely related to *Scyllium*, a form which has been studied by several writers. Although none of them has described the branchial levators, it is probable that they will be found when carefully sought for.

When the dorsal superficial constrictors are carefully freed from the fascia dorsalis, a dorsal venous sinus is exposed. This is of variable size and is particularly large in *Mustelus*. When it is opened along the length of the dorsal limit of the branchial basket and its glistening lateral wall dissected off the wall of the atriopharynx, the branchial levator sheet is exposed. This consists of five muscles; each is a thin quadrilateral muscle which takes origin above from the deep surface of the tendinous origin of the corresponding superficial dorsal constrictor, and is inserted into the fibrous strands and membranes which bind the pharyngo- and epibranchial cartilages together, but, as the ventral margin of each muscle lies above the epibranchial cartilage not far from the centre of its length, the insertion is, in the main, into that cartilage. These muscles lie one behind the other in the median wall of the gill pouches above the level of the pharynx, and in an antero-posterior vertical plane.

Innervation.—Innervation is certainly by the anterior spinal nerves, but there is, possibly, also a motor supply from the post-trematic rami of the IXth and Xth nerves.

The Epibranchial Spinal Muscles.

The epibranchial spinal muscles are constantly present in all the selachians heretofore examined. The most anterior, which, following Vetter, will be designated the subspinalis, takes origin from the ventrum of the cranium, the underside of the trunk muscles and the lateral vertebral spinous processes close thereto, and passes ventrad, caudad, and slightly laterad, to be inserted into the dorsum of the first pharyngobranchial near its posterior end. Each of the remaining three muscles takes origin from the posterior edge of the first, second or third pharyngobranchial cartilage near the joint with the epibranchial, and is inserted onto the anterior edge and dorsal surface of the pharyngobranchial behind.

These, like the branchial levator muscles, are innervated by spinal nerves.

The Branchial Adductor Muscles.

A. Dorsal.—The oblique epiarcual muscles are four in number. Each takes origin from the lateral edge of a pharyngobranchial cartilage and passes across the joint to an insertion on the posterior edge of the epibranchial cartilage of the same arch. In some species the muscles also gain attachment at the upper end to the pharyngobranchial cartilage of the arch behind, but this is always a secondary origin. The muscles lie in the angle formed between the two cartilages. The lateral edge of the pharyngobranchial is also the posterior, so that the muscles lie behind the arches.

B. Middle.—The adductores arcuum branchialium are four in number. Each is a relatively small muscle which spans the angle between the cerato- and epibranchial cartilages, each lying in front of and medial to its arch. The muscles lie close against the capsule of the joint and may be said to take origin from the epibranchial and to be inserted into the ceratobranchial.

C. Ventral.—There are no oblique subarcual muscles developed in connection with the branchial arches of any of the selachian examples examined.

Ventral interarcual muscles are not developed either in any selachian as yet examined.

Branchial Depressor Muscles.

The coraco-branchialis is a composite muscle presenting five very similar component portions. They arise together from the lateral portion of the coracoid arch or from a very strong investment of the hypobranchial spinal muscles which is attached to that arch. From this origin they diverge as they pass dorsad and cephalad on the lateral wall of the pericardium to be inserted onto the ventral surface of the first to the fourth hypobranchial cartilages. The most anterior slip of the muscle may obtain an insertion into the hypohyal, and the last commonly extends back to be inserted also into the fifth basibranchial as well as the fourth.

The Hypobranchial Spinal Muscles.

The hypobranchial spinal muscles are so essentially similar to those of *Heterodontus*, which is described in detail later, that it is quite unnecessary to describe them here.

The following table of synonymy of the hyoid and mandibular muscles is printed for purposes of check-reference.

SYNONYMY OF THE HYOID MUSCLES IN THE SELACHII.

Kesteven.	Lightoller.	Marion.	Vetter	
Csd.2a pars arcuata	Csd.2c	Csd.2	Csd.2	Dorsal
Csd.2b pars inscriptionalis	Csd.2b	Csd.2	Csd.2	
Cd.2pr. inter-branchialis	Csd.2a	Csd.2	Csd.2	
Csv.2a pars arcuata	Csv.2c	Csv.2	Csv.2	Ventral
Csv.2b pars inscriptionalis	Csv.2b	Csv.2	Csv.2	
Interhyoideus	Csv.2a	anterior part of interhyoideus	Csv.2	
Levator hyoidei	L.2	Levator hyoidei		
Coracohyoideus	Not mentioned	Coracohyoideus		

SYNONYMY OF THE MANDIBULAR MUSCLES.

Cd.1	Csd.1b″ Csd.1c	Csd.1	Csd.1
Csv.1a pars intermandib.	Csv.1a″	Csv.1	Csv.1
$Csv.1b^2$ pars extramandib.	Csv.1b″	Csv.1	Csv.1
Lev.max.sup.	L.1	levator maxillae superioris	
Pterygoideus	Csd.1a	Lev.lab.sup.	Add. B
Quadrato-mandibularis	Csd.1a + Csd.1b′ Csv.1a + Csv.1b′	Adductor mandibulae	

THE MUSCLES OF THE HYOID SEGMENT.

It will save repetition to state at the outset that these muscles are all innervated by the hyo-mandibular branch of the VIIth nerve.

THE SUPERFICIAL CONSTRICTORS.

The most detailed description of the dorsal superficial constrictor muscles in the selachians is that of Lightoller. He has described those of *Mustelus*, *Galeus* and *Orectolobus*. Whilst my own dissections enable me to confirm his descriptions, I find myself unable to accept the whole of his interpretation of the muscles.

LIST OF ABBREVIATIONS USED ON THE ILLUSTRATIONS TO PART I, SECTION 1.

Add.br., Mm.adductores arcuum branchialium ; Add.hy., M.adductor hyoidei ; B.br., Basibranchial cartilage ; Cd.1, Mandibular dorsal constrictor muscle ; Cd.2.pr., Hyoid deep constrictor, interbranchial, muscle ; Cer.br.c., Ceratobranchial cartilage ; C-g., M.coracomandibularis ; C-h., M.coracohyoideus ; C.n., Capiti-nuchal muscles ; Cor., Coracoid arch ; Cr.gl., M.cranioglossus ; Csd.2b, Pars inscriptionalis of the dorsal superficial hyoid constrictor muscle ; Csd.3-6 a & b, Partes arcuata and inscriptionalis of the dorsal superficial branchial constrictor muscles ; Csd.3.pr., The first deep branchial constrictor, interbranchial, muscle ; Csv.1a., Pars intermandibularis of the ventral mandibular superficial constrictor muscle ; $Csv.1b^2$., Pars extramandibularis of the ventral mandibular superficial constrictor muscle ; Csv.2b, Pars inscriptionalis of the ventral hyoid superficial constrictor muscle ; Csv.3-6 a & b, Partes arcuata and inscriptionalis of the ventral superficial branchial constrictor muscles ; Ct., The thick perichondrium of the symphysis ; Cu., M. cucullaris ; D.a-o.p., Dorsal antorbital process ; E.c., Ethmoid cartilage ; E.m., External branch of the hyomandibular ramus of the VIIth nerve ; Ep.br.c., Epibranchial cartilage ; Epi.o., M. epiarcualis obliquus ; Epi.sp., M. epibranchialis spinalis ; Ex.br.c., d & v., Dorsal and ventral extrabranchial cartilages ; F.1 & 2, The line of the floor of the first and second gill pouches ; G.c.1 & 2, The position of the first and second gill clefts ; H-h., M. interhyoideus ; Hy.c., Hyomandibular cartilage ; Hy.br., Hypobranchial cartilage ; Hy.br.c., Hyobranchial cartilage ; Hy.gl., M. hyoglossus ; Hy.m., Hyomandibular cartilage ; I.h. & I.hy., M. interhyoideus ; Lb.c., Labial cartilage ; L.hy., M. levator hyoidei ; L.l.i., M. levator labii inferioris ; L.l.r., The lateral ligament of the rostrum ; L.l.s., M. levator labii superioris ; L.mx.s., M. levator maxillae superioris ; Lev.hy-mn., M. levator hyomandibulae ; Lev.pal., M. levator palatini ; L.r., M. levator rostri ; L.r.r., Ligamentum radicis rostri ; Mck. & Mn., Meckel's cartilage ; Md.l., M. mandibulo-labialis ; Mn.V., The mandibular ramus of the Vth nerve ; Mx.l., M. maxillo-labialis ; Op., Opercular flap ; Op.r., Opercular rays seen through the flap ; P.l.s., M. protractor labii superioris ; P.s.l.i., M. protractor superior labii inferioris ; Pt., M. pterygoideus ; Pty.a. & p., Partes anterior and posterior of the M. pterygoideus ; Qm., M. quadratomandibularis ; Qm.a., p. & v., Partes anterior, posterior and ventralis of the M. quadratomandibularis ; R., Superficial raphe ; Sp., The spiracle.

The roman numerals indicate the appropriate cranial nerve or its foramen, V^1, V^2 & V^3, the three rami of the Vth nerve.

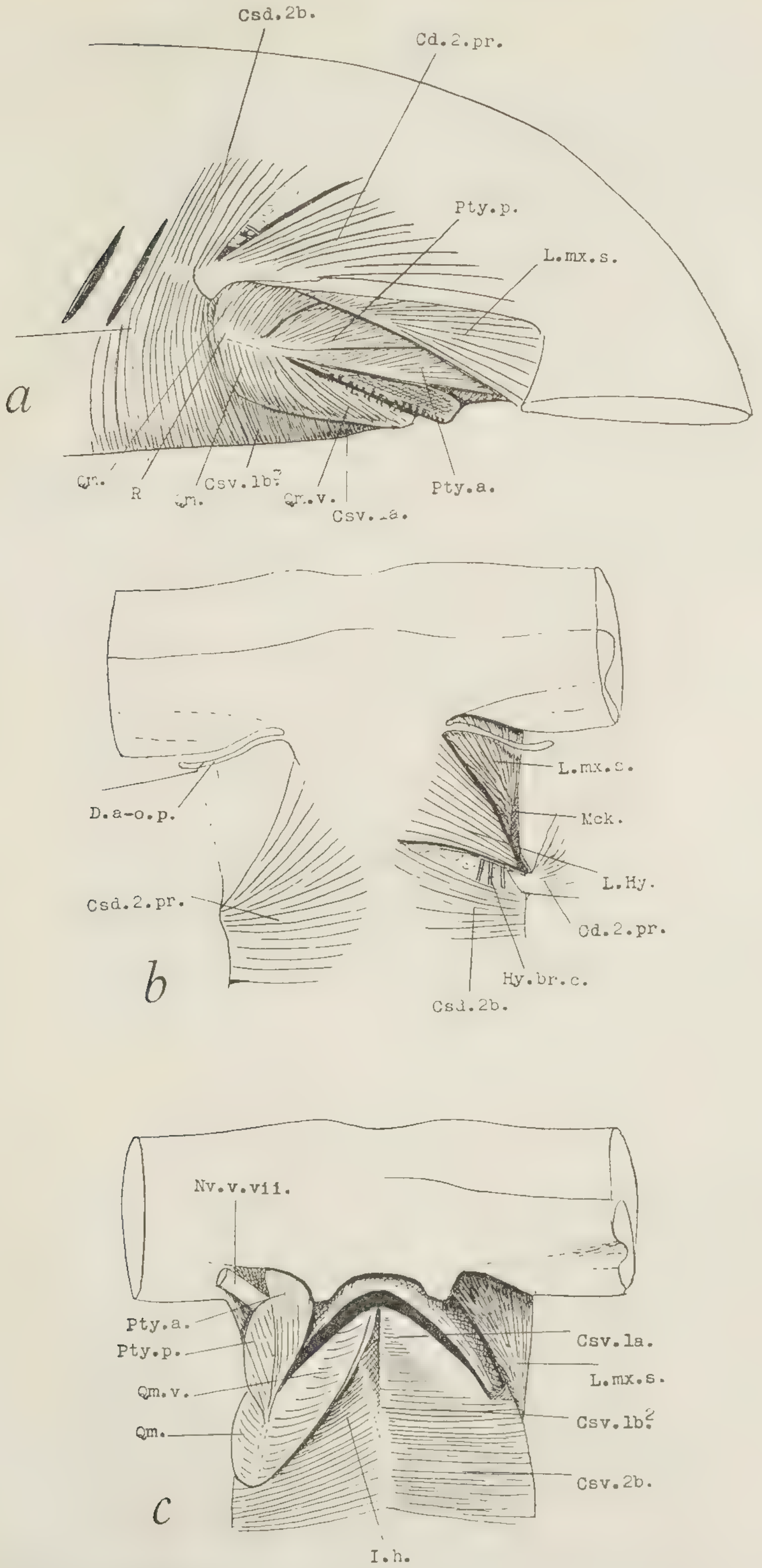

Csd.2b.
Cd.2.pr.
Pty.p.
L.mx.s.
a
Qm.
R
Qm.
Csv.1b²
Qm.v.
Csv.1a.
Pty.a.
L.mx.s.
D.a-o.p.
Mck.
L.Hy.
Csd.2.pr.
Cd.2.pr.
Hy.br.c.
Csd.2b.
b
Nv.v.vii.
Pty.a.
Pty.p.
Qm.v.
Qm.
Csv.1a.
L.mx.s.
Csv.1b²
Csv.2b.
c
I.h.

Fig. 4.—The hyoid and mandibular muscles of *Sphyrna*. A, lateral; B, dorsal; and C, ventral views. The right side more deeply dissected than the left.

A. Dorsal.—The superficial dorsal hyoid constrictor is essentially similar to the branchial muscles. There is, however, no similar muscle anterior to it, so that whilst there is the community of origin between the pars arcuata of this and the pars inscriptionalis of the muscle behind—the first dorsal superficial branchial constrictor—there is no similar common origin of two muscles dorsal to the spiracular cleft. The origin of the two portions of the muscle is from the fascia dorsalis posterior to the spiracle, and separated therefrom by the deep constrictor, which has acquired a superficial position. Ventrally the muscle is, in conformity with the superficial constrictors behind it, either continued more or less uninterruptedly over into the ventral constrictor or interrupted by the insertion of more or fewer of its fasciculi into a prominent middle gill-ray.

B. Ventral.—The ventral hyoid superficial constrictor also is essentially similar to the branchial constrictors behind it, and its origin medially is either from a median ventral raphe, and this is the commonest condition, or from the aponeurotic investment of the hypobranchial spinal muscles.

The Deep Hyoid Constrictors.

A. Dorsal.—This is represented by that anterior portion of the superficial dorsal constrictor which lies against the inner ends of the pseudo-hyoidean gill rays. A careful analysis of the musculature of the interbranchial muscles and their related partes inscriptionales will demonstrate that the latter cannot be regarded as extending deeper on the septum than the outer ends of the gill rugae. At this depth, if not more superficially, it is commonly found that there is a change in the texture of the fasciculi, the deeper being the finer, and in most forms there is, in addition, above and below, a very readily demonstrable difference of direction, and/or origin and insertion. Now in the hyoid dorsal superficial constrictor in the selachians one finds that, in every instance, the portion of the muscle which Lightoller designates pars inscriptionalis extends forward and deeply, quite uninterruptedly, till it comes to lie in contact with the deep ends of the pseudo-hyoidean gill rays, with the gill rugae on the other side of those rays. That is to say, its most anterior portion occupies a position relative to the gill rays and filaments which, in the branchial segments, is occupied by the deep constrictors.

The origin of the muscle is from the fascia dorsalis, its insertion being into the loose fibrous tissue which separates the posterior margin of this muscle from the pars extramandibularis of the first ventral superficial constrictor. Posteriorly the muscle is, as already stated, quite inseparable from the pars inscriptionalis of the superficial constrictor. Anteriorly above it blends, without limiting margin, with the hyoid levator; below it is limited by its own loose perimysium, by which it is separated from the insertion of the hyoid levator and from the insertion of the pars extramandibularis, Csv.1b^2.

Briefly the contention here is, that the muscle which previous workers, except Lightoller, have designated the superficial dorsal constrictor of the hyoid segment, is *that* muscle plus the interbranchial muscle or deep dorsal constrictor of the segment.

The truth of this contention is most strikingly proven by the muscle in *Chiloscyllium*.

Commencing at the posterior margin of the muscle there is first a typical pars arcuata, which arises in common with the pars inscriptionalis of the first dorsal superficial branchial constrictor. In front of this, and perfectly continuous with it, is a typical pars inscriptionalis. The pars arcuata is covered on the deep surface as well as on the superficial by the skin. The pars inscriptionalis is covered superficially by skin, but has the outer free ends of the hyoidean gill rays against its deep surface, with the outer ends of the gill rugae on the other side of these rays. The anterior margin of the pars inscriptionalis is a slightly curved line which commences, at the common level of the dorsal superficial constrictors, above and a little forward of the first gill slit. From this point it passes ventrad and cephalad to the posterior margin of the outer end of the hyo-mandibular cartilage. There is along this line a narrow ribbon of fascial tissue from which the fibres of the pars inscriptionalis appear to take origin, and which also separates the anterior margin of the pars inscriptionalis from the hyoid levator in front of it. When, however, the fibres of the pars inscriptionalis which appear to arise from the narrow ribbon are carefully dissected free from it, they are found, every one of them, to turn mediad and pass deeply between the posterior surface of the hyoid levator in front and the deep, attached ends of the hyoidean gill rays behind them. These fibres are beyond doubt completely homologous with the fibres of the deep branchial dorsal constrictors. Like them, they provide a muscular layer for the anterior wall of the branchial pouch in its depth, and arise from structures along the dorsal fornix of the depth of the pouch.

They also reproduce very faithfully the conditions found in the anterior wall of the first gill pouch in the rays.

In *Sphyrna* (Figs. 4, A, B and C) the pseudo-hyoid and the hyo-branchial rays are very superficially placed throughout their length. The Cd.2.pr. arises from the fascia dorsalis, reaching almost to the mid-dorsal line and so far forward as to lie almost above the anterior margin of the lower jaw. The fibres are directed caudad and ventrad and are inserted into the subdermal tissues attached to the outer end of the hyo-mandibular. The first branchial pouch is continued far forward above the mouth, almost so far as the anterior margin of this Cd.2.pr. These fibres, however, are not in contact deeply with the hyoid gill rays, except just a few of them along the posterior margin of the muscle. Whilst the hyoid levator appears to have retained its normal origin from the skull, at the posterior margin of the orbital region, the absence of spiracle and of the orbital structures has permitted the first branchial pouch to grow forward beneath it, capturing the spiracular space. The Cd.2.pr. has grown forward, but superficially to the levator. It is significant, however, that none of the fibres are superficial to the levator muscle at their insertion.

The Cd.2.pr. grows forward over the levator hyoidei in *Carcharhinus* also. In this form the two muscles are fused along their anterior margins but are readily separable posteriorly. It is worthy of note that this peculiar forward growth of the Cd.2.pr. superficial to the hyoid levator was found only in these two genera which are both devoid of a spiracle. Lightoller has described the muscle in *Carcharhinus* under the designation pars epihyoidea (Csd.2a) of the second superficial dorsal constrictor.

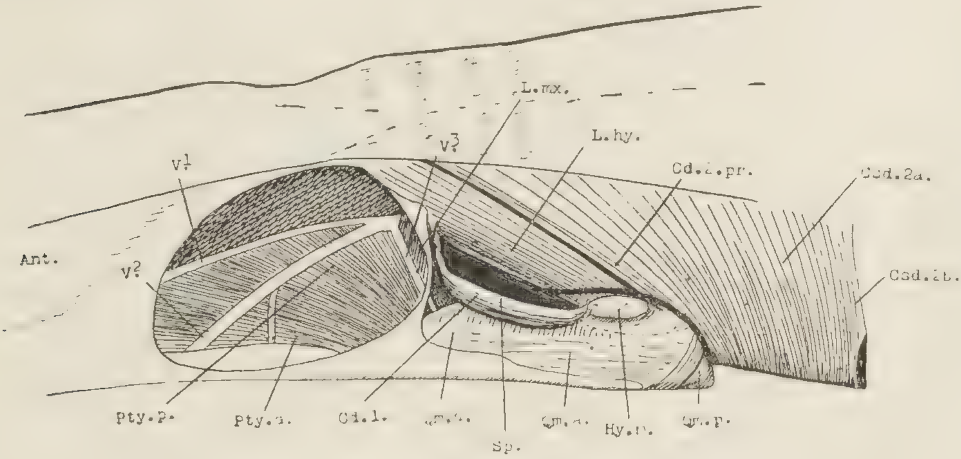


Fig. 5.—Some of the hyoid and mandibular muscles of *Pristiophorus*. Lateral view.

Pristiophorus (Fig. 5).—The superficial dorsal constrictors arise from the fascia dorsalis along a line which is level with the upper margin of the orbit in front and slopes ventrad as it extends backwards. This is the line of origin, not only of all the superficial dorsal constrictors, but also of the hyoid levator in front of them, and the swelling of the muscles immediately below their origins causes a longitudinal sulcus along the line of origin which is quite obvious before the skin is removed. The anterior limit of Cd.2 is over the middle of the spiracle, the posterior limit directly dorsal to the first gill slit. The most anterior fasciculi of the Cd.2.pr., some half dozen or so, slope ventrad and caudad to be inserted into the subcutaneous tissue over the outer end of the hyo-mandibular. Behind these a narrow band of fasciculi is inserted into the quadrate itself just below the joint with the hyo-mandibular cartilage. The most posterior fibres, also quite a few fasciculi, are inserted behind these last into the hyo-branchial rays. Fibres immediately behind these belong to the pars inscriptionalis.

The anterior margin is in contact with the posterior margin of the levator hyoidei, but there is no fusion of the two muscles; they may be cleanly and readily separated from origin to insertion.

In *Acanthias* and *Mustelus* the muscles fit the general description given above.

The Cd.2.pr. in *Mustelus* is somewhat peculiar in that it blends indefinitely with the hyoid levator in front of it. Lightoller finds a cleavage plane parallel to the surface which divides the levator into superficial and deep portions. The superficial portion he regards as the anterior "pars epihyoides" of the Csd.2. The deep portion alone he identifies as the levator. The cleavage plane which he describes is undoubtedly present, but I am not able to satisfy myself that it is not fictitious. With a view to determining this point I have dissected four individuals. In the eight muscles thus dissected I have found a single clean cleavage in four, two such in one, and three such in three. In each case the anterior limit of the muscle was determined on each side and the head was then cut right through in the transverse vertical plane immediately in front of the muscle, then cut through in the same plane at the first gill slit. It was next divided down the mid-sagittal plane. The muscle was then cleaned both on its superficial and deep surfaces, and cleavage planes sought for. None was accepted as a cleavage plane unless no fasciculi were severed in the separation of the two portions of the muscle.

Both Vetter and Marion state that in *Acanthias* a large portion of the anterior fibres of the Csd.2 are inserted into the dorsal and posterior edge of the quadrate end of the palate quadrate. Vetter and Marion described *Acanthias vulgaris*; I have worked on the allied species *A. megalops* Macleay. In this form I find that only two fasciculi on each side are inserted into the back of the palate quadrate, and that the remainder pass deeply under the fibrous tissues, into which they appear to be inserted, behind the jaw, and are either inserted into the bases of two or three of the hyoidean gill rays or are continued ventrad into the pars profunda of the ventral constrictor of the hyoid segment.

The apparent difference arises from the fact that both these authors regard the hyoid levator as the anterior portion of the hyoid constrictor.

The Pars Epihyoidea.—This term was introduced by Lightoller to designate the anterior portion of the dorsal constrictor sheet in the hyoid segment. As already stated, he regarded this as the anterior portion of the superficial constrictor, whilst I have just been describing it in detail as the pars profunda of the sheet, or the deep constrictor.

It is a fact that in a majority of the examples studied more or fewer of the fibres of the muscle are inserted into either the outer end of the hyomandibular or the posterior edge of the quadrate portion of the palatoquadrate or into both. The number of fibres so inserted is, however, very variable and in some instances none of the fibres are so inserted. This variability, taken in conjunction with the fact that throughout the whole of the batoid plagiostomes none of the fibres of the pars profunda of the dorsal hyoid constrictor have an insertion onto either of these two cartilages, leads me to regard the insertion as of entirely secondary importance.

In other words it is not regarded as an inherited feature, but rather as an individually acquired feature resulting from the mechanical or spatial conditions imposed by the variations in the skeletal structures.

B. Ventral.—The interhyoideus is a narrow strap-like muscle which takes origin from a relatively extensive length of the ventral median raphe under cover of and in contact with the first ventral superficial constrictor. From this origin the muscle tapers to a short rounded tendon which is inserted into the contiguous ends of the hyomandibular and ceratohyal cartilages. The proportion of fibres inserted into each is variable, but the greater number in all the examples studied are inserted into the lateral end of the ceratohyal.

The anterior margin of this muscle is always clearly defined and the separation of the muscle from the overlying Csv.1 is quite easy and definite, but posteriorly it becomes gradually fused with the superficial layer. In some forms this fusion implicates the pars extramandibularis of the first ventral constrictor, but in the majority of the examples it was possible to separate the muscle completely therefrom. On the other hand, in no case was it possible to define the posterior margin of this hyoid deep ventral constrictor from the anterior margin of the pars inscriptionalis of the superficial ventral hyoid constrictor. This fact has led to the muscle being treated, by previous observers, as the anterior portion of the superficial constrictor of the hyoid segment.

Undoubtedly it is part of the primitive constrictor sheet, but it is the deeper part, completely comparable with the dorsal deep constrictors of the branchial segments, each of which lies in continuity with the more superficial portion of its own sheet behind it.

THE HYOID LEVATOR.

Sphyrna (Fig. 4, B).—The hyoid levator in *Sphyrna* is an unique flat triangular muscle, with a thin posterior and thicker anterior margin. It arises in common with the pars profunda of the Cd.2, though not extending quite so far back as that muscle. It has also an origin from the vestigial antorbital process and from the perichondrium of the skull in front of this last. Its fibres pass ventrad and caudad, but at an angle with those of the pars profunda, to be inserted along the posterior half of the dorsal edge of the lateral surface of the hyomandibular cartilage.

The relation between this muscle and the deep constrictor, superficial to it, at their origin is of some interest. Actually they have preserved the relation of the branchial levator and deep constrictor.

It will be remembered that the superficial dorsal constrictors arise from the fascia dorsalis, but that the pars inscriptionalis of each is interrupted by a tendinous intersection which is attached to the dorsal extrabranchial cartilage. Now, the levator passes down on the medial wall of the branchial pouch taking origin above from the tendinous origin of the superficial constrictor. It, therefore, passes, and is bound to, the medial edge of the deep end of the extrabranchial cartilage. The interbranchial muscle takes its origin from the inferior edge of this same cartilage.

In the branchial segments the presence of the pharyngo-branchial cartilage limits the dorsal extent of the gill pouch. In the hyoid segment of *Sphyrna* there is no cartilage to stay the dorsal extension of the pouch which has therefore been able to rise internal to the levator as well as the constrictor.

Pristiophorus (Fig. 5).—The hyoid levator in *Pristiophorus* lies anterior to and parallel with Cd.2.pr. Superficially it is in series with the constrictors, but extends more deeply. It takes origin in front of Cd.2.pr. from the tendon of insertion of the trunk muscles into the skull, and from the post-orbital process and the side of the auditory capsule, extending deeply, almost to the ventrum of the skull behind the orbit. It is inserted onto the dorsal edge of the outer two-thirds of the length of the hyomandibular cartilage. This is a thick fleshy muscle which provides the full depth of the posterior wall of the spiracle lying between that cleft and the anterior wall of the first gill pouch.

Innervation.—This is by two or three twigs which leave the hyomandibular ramus of the VIIth nerve as it winds laterad, caudad and superficiad across its anterior surface under cover of the skin, on the posterior wall of the spiracle.

Chiloscyllium (Fig. 6).—In *Chiloscyllium* the muscle is placed in front of the pars profunda of the constrictor, which, as already described, turns deeply in contact with its posterior surface. The levator is a compact thick muscle which arises from the side wall of the auditory capsule and passes cephalad, laterad and ventrad to the outer end of the hyomandibular cartilage. Its relation to the spiracle and its nerve supply are as in *Pristiophorus*. In fact so constant is this relation that it will not be repeated in the descriptions which follow.

Acanthias is essentially similar to *Chiloscyllium*.

Mustelus.—In *Mustelus* the levator is not definable from the pars profunda of the constrictor sheet behind it. For the purposes of description it is assumed that the fibres inserted into the outer end of the hyomandibular alone are levator fibres. If this assumption be granted, then we may briefly describe the levator of *Mustelus* as differing from that of *Pristiophorus* only in that the peculiar backward extension of the tensor palpebrae muscles lies between the levator and the skull, and occupies some of the space on the skull side wall that, in *Pristiophorus*, the levator arises from.

The Hyoid Depressor Muscle (Innervated by spinal nerves).

The coracohyoideus muscle is in series with the components of the coracobranchialis. The origin is from the coracoid lateral to the origin of the coracomandibularis and from the aponeurosis on the lateral and deep surface of this muscle. In some examples the origin from the coracoid is only indirect through the aponeurosis. The muscle is one of the largest of the hypobranchial spinal muscles, and its insertion is on to the hyoid copula just behind the lower jaw.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Constrictors.

The excessive development of the middle adductor of this segment, to form the muscles of mastication, has, apparently, been responsible for the complete suppression of the middle fibres of both dorsal and ventral constrictors, so that they do not meet in the midline anywhere. Further, the dorsal constrictor has been crowded against the levator so that the two muscles are, at times, fused together.

A. Dorsal.—As might have been anticipated, this muscle is least modified in those forms with the largest spiracular apertures, such as *Pristiophorus*. In this genus the dorsal constrictor, Cd.1, takes the form of a well developed constrictor spiraculi (Fig. 5, Cd.1). It is a thin sheet of fasciculi which supplies the greater part of the thickness of the anterior and lateral wall of the widely open spiracle. An arcuate ridge around the anterior and lateral edge of the spiracle, formed by this muscle, is quite obvious before the skin is removed.

The muscle arises from the antero-lateral edge of the auditory capsule below the post-orbital process and in front of the origin of the M. levator hyomandibularis. From this origin the muscle trends horizontally, first laterad, then caudad, and finally mediad round the outer margin of the spiracle, to be inserted into the hyomandibular just above and medially to the hyomandibulo-palatoquadrate joint.

In *Acanthias*, *Orectolobus* and *Brachaelurus* the Cd.1 is essentially as in *Pristiophorus*, but in these other genera the spiracle is much smaller.

In *Mustelus* the muscle presents division into a more superficial and a deeper portion. The former is again divided into a superficial and a deep part. The last takes origin from the fibrous tissue about the upper end of the hyomandibular cartilage, above and behind the spiracle and, running forward, terminates in a fine tendon which is inserted into the upper eyelid at the outer posterior canthus. The superficial portion is a much larger component, which takes origin from the ventro-lateral portion of the occipital part of the skull deep to the origin of the second levator. This also runs forward and its terminal tendon is inserted into the lower eyelid, also at the outer canthus.

The deeper portion of this muscle is closely adpressed to the levator maxillae superioris and appears fused with it. Careful dissection reveals that superficially to the levator there is a muscle which may always be cleanly separated from it. The bulk of this muscle lies posteriorly to the levator; it arises from the posterior edge of the post-orbital process and is separately inserted onto the outer margin of the upper surface of the palatoquadrate.

Mustelus is, in respect to its Cd.1, intermediate between the species with large spiracles and those devoid of the spiracle. In these last, *Sphyrna* and *Carcharhinus*, the whole of the muscle is modified to act upon the eyelid; in *Mustelus* only portion is so modified.

Lightoller* (1939, p. 348) designates this the pars cranio-maxillaris of the muscle and failed to find the more normal part in *Mustelus*; he failed to separate it from the levator (*l.c.*, Pl. II, fig. 6).

In *Chiloscyllium* the Cd.1 is very similar to that which we have just discussed in *Mustelus*. It is a small thin sheet of muscle which takes origin from the outer edge of the auditory capsule at the back of the orbit, and passes cephalad, laterad, and slightly ventrad, to be inserted into the superior margin of the quadrate portion of the palatoquadrate. Immediately in front of, and deep to, it is the small first levator, separated by a short but quite definite interval.

Innervation.—Norris and Hughes (1920, p. 337) state that in *Squalus acanthias*, "From the dorsal border of the main trunk of the ramus mandibularis (V) shortly after leaving the ganglion there are given off a few (three or four) small branches, which break up into numerous small twigs, motor elements supplying the levator palatoquadrati and spiracular muscles". This levator palatoquadrati can be none other than the levator maxillae superioris which, as Marion has stated (1905), is confluent with the "Csd.1". I have found a similar innervation for the two muscles in *Pristiophorus*, *Chiloscyllium* and *Brachaelurus*, and I find the large levator maxillae superioris of *Sphyrna* to be similarly innervated.

My own dissection notes on *Pristiophorus* read as follows: The innervation (of the levator maxillae superioris) is from the mandibular ramus of the Vth nerve by a relatively large twig which leaves the ramus, just after that leaves the other rami, and plunges into the anterior surface of the muscle. A fine twig of this nerve was followed right through the muscle and found to terminate in a twig that had been observed passing from the posterior surface into the Cd.1. This confirms the findings of Vetter (1874).

For reasons which are stated later, this Cd.1 is regarded as being homologous with the deep constrictors of the branchial segments, the interbranchial muscles.

---

* The pars nucho-maxillaris of Lightoller is the muscle which has been identified in this work as the M. adductor hyoidei in *Heterodontus*. It is innervated by the facial nerve. This muscle has not been found in any Selachian, but it is believed that its homologue is very generally present in the Batoids, where also it is innervated by the facial nerve.

B. Ventral.—The intermandibularis muscle of the selachians takes origin on each side from the inferior and posterior edge of the lower jaw and is inserted into a median ventral raphe. In most instances it is possible to recognize anterior, intermandibularis, and posterior, extramandibularis, portions of the muscle, Csv.1a and Csv.1b². The former takes origin entirely from the edge of the jaw, whilst the latter extends laterad and dorsad over the cartilage of the jaw to take origin in the aponeurosis of the quadrato-mandibularis. It should be understood, however, that in most examples this distinction is more or less arbitrary and that no definite line of cleavage between the two parts can be demonstrated.

More or fewer of the anterior fasciculi may be quite continuous from one side to the other. I find this condition in *Squalus* and *Brachaelurus*, and Lightoller finds a relatively araphic portion of the muscle in *Mustelus* and *Orectolobus*. The araphic portion is not present in *Carcharhinus*, *Sphyrna* or *Pristiophorus*. The presence of an araphic "M. submentalis" developed from the fifth muscle plate in the great majority of the vertebrata above the Elasmobranchs gives to these araphic fasciculi in some of the Sharks an added importance and significance.

Innervation.—The anterior and posterior portions of the muscle are both innervated from the terminal twigs of the mandibular ramus of the Vth nerve. There is also some motor (?) supply to the posterior portion from the ventral terminal twigs of the hyoid branch of the ramus hyomandibularis of the VIIth nerve.

THE LEVATOR.

As in the segments behind, the levator arises in close association with the deep constrictor, and in most instances the two muscles are inseparable at their origin. Actually the levator takes its origin deep to and in front of Cd.1, from the side wall of the auditory capsule in the majority of examples studied, but in some genera departs widely from this apparently more normal condition.

In six of the eight selachians dissected the levator maxillae superioris is a relatively small rounded, oval or flat muscle which arises from the side of the auditory capsule either just in front of the lateral angle so as to be within the orbit or just behind the orbit. From this origin it passes ventrad commonly with an inclination laterad and caudad to be inserted on the dorsal surface of the palatoquadrate.

In *Sphyrna* (Fig. 4) and in *Carcharhinus*, one of the forms dissected by Lightoller, the muscle is much more extensively developed.

Sphyrna (Figs. 4, 6; L.mx.s.).—The levator maxillae superioris is a massive flat triangular muscle which takes origin from the posterior edge of the proximal portion of the inferior antorbital process and from the side wall of the skull from that process back to the hyomandibular articulation. This latter area, along the side of the skull, is along the whole of the length where, normally, the structures of the orbit are situated. The origin is placed above the exit of the optic nerve and the origin of the extremely tenuous tendons of the oculomotor muscles. The lateral edge of the muscle is quite thin at the origin and these lateral fibres run almost directly caudad to their insertion. The posterior, medial margin of the muscle is thick and these fibres run nearly directly laterad to their insertion. The whole of the fibres converge to an insertion onto the capsule of the hyomandibulo-maxillary joint and onto the quadrate in front of the joint.

Innervation.—This, in my experience, is always by twigs from the mandibular ramus of the Vth nerve. This nerve always lies in front of the muscle altogether, or, as in such forms as *Sphyrna* in which the muscle is more extensive than usual, it lies beneath the muscle. The maxillary ramus of the Vth nerve in these forms runs to its destination between the levator maxillae superioris, placed superficially or dorsally to it, and the pterygoideus, situated medially or ventrally to it.

THE ADDUCTOR MUSCLES.

Two of the primitive adductors are recognizable in the mandibular segment, namely, the epiarcual oblique and the middle adductor. It is believed that the former is completely homologous with the pterygoideus muscle of higher forms, and it will be described under that designation. The middle adductor will be designated the quadrato-mandibularis, a name adopted from Lightoller. It is believed that it presents the fore-runners of more than one of the adductor muscles of the mandible of higher forms and, since the term adductor mandibularis of Vetter, Marion and other previous workers includes that which I designate the pterygoid, it seemed desirable to make use of another name and one that had not been applied to any of the muscles present in the higher forms. Lightoller included the "pterygoideus" under his designation, but, as it has not been generally adopted, its use is not so liable to convey a misconception as would the use of any designation already generally adopted.

The Pterygoideus* (Epiarcual Oblique) Muscle.

This is the muscle which Vetter designated Add. β and to which Marion applied the name levator labii superioris, adopting a suggestion by Vetter that the muscle were more correctly included among the superficial constrictor muscles. Lightoller describes the muscle with the quadrato-mandibularis and regards it as being an undifferentiated portion of the first dorsal superficial constrictor. He designates it Csd.1a.

Typically, that is to say, in the majority of the examples studied, the pterygoid muscle arises from the ventrum of the skull in front of the mouth, usually from the nasal capsule or from some process thereof. The origin is relatively extensive and the fibres converge to a tendon which is inserted into the mandibular cartilage immediately behind the gape. This insertion may extend down across the outer face of the cartilage to its median inferior edge. Always on the outer, superficial, surface of the mandible, the insertion may be confined to the upper edge or may be in part into that edge and in part into the tendinous raphe which is commonly found strongly developed on the surface of the quadrato-mandibularis muscle or at close to the angle of the gape of the jaws.

The muscle always presents two component parts, which may be more or less completely blended along their contiguous surfaces or may be readily and quite cleanly separated along those surfaces. At and close to their insertions the two portions are always blended.

In the majority of those examples in which the superior labial cartilages are well developed this pterygoideus muscle is intimately bound to the upper of the two.

In *Acanthias megalops* (Fig. 7) I find the pterygoideus muscle to be essentially similar to that of *Acanthias vulgaris* as described by Marion. It takes origin from the inferior surface of the skull to one side of the midline a little distance behind the nasal capsule. It is a rounded muscle and proceeds laterad with a slight curve caudad till it reaches the angle of the gape; here it crosses the palatoquadrate and terminates in a fine strong tendon which penetrates the quadrato-mandibularis, and becomes lost as it breaks up among those fasciculi of that muscle, which are inserted into the tissues of the side of the mouth. Near its origin, the ventral surface of the muscle is intimately bound to the upper labial cartilage, whilst its concave posterior surface lies against the front of the palatoquadrate.

The superior maxillary division of the fifth nerve crosses the muscle just behind its origin. The mandibular division crosses the palatoquadrate some distance further back and divides into two branches, one of which passes ventrad in front of the quadrato-mandibularis and, crossing the tendon of the pterygoid muscle, ends in the deep fascia beneath the skin behind the jaw and innervates the Csv. (Norris and Hughes). The other branch burrows beneath the adductor and will be described later.

Careful dissection reveals that the muscle is composed of two parts: (1) A pars anterior which arises as just described and which is inserted onto the anterior tip of the labial cartilage. This portion is very short. (2) A pars posterior arising from the upper surface of the labial cartilage and inserted as just described.

In *Mustelus* (Fig. 8) the origin of the pterygoideus muscle is much more extensive: (i) from the greater part of the posterior wall of the nasal capsule; (ii) from the inferior surface of the floor of the same capsule along a line, immediately in front of the attachment of the palatoquadrate thereto, which extends from the lateral edge almost to the midline; (iii) from the lateral edge of the ethmoid process on the dorsum of the palatoquadrate behind the nasal capsule. The superficial fibres of the muscle are inserted into the anterior end of the median superficial raphe of the quadrato-mandibularis; the deeper fibres are gathered into a fine strong cord-like tendon which burrows beneath the superficial fibres and is inserted into the tissues of the side of the mouth. When the muscle is released from its origin, it is found that the portion which arises from the posterior wall of the nasal capsule provides practically all the deep fibres and that this portion is incompletely separable from the rest, and further, that when that separation has been effected, the appearance is that one has thus separated a muscle which completely corresponds with the pars anterior of *Acanthias*, and that the remainder of the muscle is the pars posterior. The superficial fibres take origin, not only from the other situations but also from a band of tendinous fibre which connects them and arches over the deeper portion without being bound thereto. Fusion of the superficial and deep portions commences a short distance behind this band and becomes more definite as the quadrato-mandibularis is approached.

---

* See discussion on this designation on p. 60.

The maxillary division of the fifth nerve crosses the surface of this muscle in front of the band uniting the origins of its superficial portion. The mandibular division of the nerve plunges out of sight between this muscle and the quadrato-mandibularis under cover of a strong band of fibrous tissue which unites the muscle superficially along their line of cleavage. On separating the muscles, the nerve is found proceeding backward and medially parallel to the cleavage plane, imbedded in the anterior face of the quadrato-mandibularis, and here it gives off the motor branches to the muscle. At the angle of the mouth it crosses the tendon of the pterygoid muscle and breaks up into its terminal branches to the tissues on the ventrum of the mouth and to Csv.1.

Sphryna (Fig. 4, Pty.a., Pty.p.).—The pterygoideus in this form is very nearly completely divided into its two components. The pars anterior (Pty.a.) is a relatively thick short muscle which arises from a pocket formed, at the anterior end of the orbital region of the skull, by the cranium itself medially, the lateral " hammer-head " process ventrally, and the inferior antorbital process in front. The muscle tapers rapidly as it passes caudad with a slight inclination laterad. It is clothed on its median surface by the tendon into which its fasciculi are inserted. The tendon continues caudad, crosses the upper jaw in the fold of the upper lip just in front of the angle of the mouth. At the angle of the mouth it breaks up into a brush of fine tendrils which attach it to the fascial structures of the quadrato-mandibularis, and of these especially to the transverse raphe which crosses it from the gape to the Q-M. joint.

The pars posterior (Pty.p.) arises from the lateral and inferior surface of the palatoquadrate for about the centre one-third of its length. It is a blunt-ended spindle-shaped muscle similar to the pars anterior and, like it, is clothed on the median and inferior surface by a tendon into which its fasciculi are inserted and which serves very efficiently to separate it from the pars anterior for the greater part of their contactual surfaces. The tendon is inserted into the superficial raphe of the quadrato-mandibularis in common with that of the pars anterior. Most of its fasciculi are inserted into its own tendon, but those arising from the palatoquadrate close to the posterior end of the area of origin are inserted into the tendon of the pars anterior, which lies ventral to it at this point. The dorsal surfaces of both parts of the muscle are in contact with the ventral surface of the levator maxillae superioris.

Innervation.—This is by a branch of the mandibular ramus of the fifth nerve which leaves the main ramus just after that separates from the maxillary ramus.

Pristiophorus (Fig. 5).—Here, too, the pterygoideus is very completely divided into its two components.

The pars anterior (Pty.a.) is quite a small group of fibres which arise by a fine tendon from the apex of a spur which projects posteriorly from the middle of the inferior and posterior edge of the nasal capsule. The tendon is continued down the lateral edge of the muscle as well as investing its tenuous apex. The fasciculi are inserted onto the lateral edge of the tendinous investment of the posterior end of the pars posterior.

The pars posterior (Pty.p.) is a very massive muscle. It arises from the inner edge of the spur from which the pars anterior arises, and from the lateral half of the inferior surface of the nasal capsule and skull back to the articulation of the ethmoid tubercle of the palatoquadrate with the skull. From this extensive origin the fibres pass caudad and laterad, converging to be inserted into a broad tendinous sheath which invests the medial and inferior surface of the posterior one-half of the length of the muscle. This tendon lies against the inferior edge of the lateral surface of the palatoquadrate, and anteriorly and medially the thick, rounded posterior edge of the muscle lies in a broad sulcus on the anterior surface of the palatoquadrate. The tendon passes behind the angle of the gape and is inserted onto the outer surface of the mandible medial to the insertion of the quadrato-mandibularis.

Innervation.—This is from the mandibular ramus of the fifth nerve by a branch which leaves the main ramus and crosses forward and ventrad onto the upper surface of the pars medialis.

The main ramus runs caudad and mediad along the posterior edge of the pars medialis and then dips under the anterior edge of the pars anterior of the quadrato-mandibularis along the fissure between the two muscles. Behind the angle of the gape the muscles become intimately blended and here the nerve burrows under the tendon of the pterygoideus and turns forward and superficiad. The motor twigs to the quadrato-mandibularis are given off by the nerve whilst it lies in the fissure.

Chiloscyllium (Fig. 6).—This is one of the most interesting and instructive forms that have been dissected. In this genus we find the pterygoid passing up onto the dorsum of the cranium just as it does in *Chimaera* and as in *Neoceratodus* and the Tetrapoda generally. Particular attention is drawn to these several forms because it is believed that there is no room for doubt that the pterygoideus muscle of *Chiloscyllium* is completely homologous with the other pterygoideus muscles just described; it is also believed that the study of *Chimaera* and *Neoceratodus* leads us naturally to the identification of the same muscle in the Axolot and finally in the amphibians and tetrapods generally.

The pars anterior is here much the larger of the two parts (Fig. 6, Pty.a.). It arises from (i) the dorsum of the skull medially to the orbit and as far forward as the nasal capsule, (ii) from the front of the antorbital process, (iii) from the posterior wall of the nasal capsule, and (iv) from the side of the skull between these last two. This remarkable massive muscle is clothed along its postero-medial (deep posterior) edge by a strong tendinous sheath into which its fasciculi are inserted. The tendon crosses the palatoquadrate behind the angle of the mouth, then crosses Meckel's cartilage between the partes ventralis and posterior of the quadrato-mandibularis muscle and is inserted into the inferior, postero-medial, edge of the cartilage.

The pars posterior (Fig. 6, Pty.p.) is a quite small muscle which arises from the lateral and inferior corner of the antorbital process. The fibres of this muscle are inserted close together onto the posterior edge of the tendon of the pars anterior as that tendon crosses the palatoquadrate.

Innervation.—This is by a branch of the ramus mandibularis of the Vth nerve which leaves the main trunk just as that nerve reaches the upper margin of the palatoquadrate at the anterior and inferior margin of the orbit. The main nerve then continues on its way against the anterior surface of the quadrato-mandibularis and beneath the tendon of the pterygoideus and fibres of its pars posterior. It burrows beneath the tendon of the pterygoideus and turns mediad and superficiad.

THE QUADRATO-MANDIBULARIS (MANDIBULAR ADDUCTOR) MUSCLE

In general terms this muscle may be described as a complexly arranged mass of muscle fasciculi which arises from the quadrate portion of the palatoquadrate and are inserted into Meckel's cartilage, and, indeed, it is essentially in this manner that previous workers have described it.

The careful comparative study of many forms, however, leads one to the discovery that there is, underlying the apparently orderless arrangement of the fibres, one fundamental plan.

Each of four component "parts" is quite definitely recognizable in more or fewer of the types that have been studied. On the other hand, in no one of these are all four of those parts completely separable one from the other, neither is there any one of them in which all the four parts are not recognizable and definable to some degree at least.

In general terms the parts may be described as follows: (1) Pars posterior. This arises from the posterior portion of the quadrate end of the palatoquadrate, and its fibres pass directly across the axis of the Q-M. joint to be inserted on the posterior end of Meckel's cartilage.

(2) Pars medialis. The fibres arise from the deep surface of an aponeurotic sheet on the surface of the muscle, which may or may not be attached to the cranium dorsally, and they may be inserted onto Meckel's cartilage along its posterior edge or they may blend absolutely inseparably with the fasciculi of the partes posterior and anterior which lie behind and in front of them. When the part retains its individuality it may be quite superficial and be inserted only along the edge of Meckel's cartilage, or it may burrow deeply between the other two parts to an insertion on the outer surface of the cartilage.

(3) The pars anterior takes origin from the quadrate in front of the pars posterior. Its fibres, in the majority of instances, have an inclination to the plane of the palatoquadrate arcade as they pass ventrad, to be inserted into Meckel's cartilage in front of the pars posterior.

(4) The pars ventralis (Add. μ of Vetter). This portion is best developed in those forms in which the long axis of the jaws from joint to symphysis approaches most closely the long axis of the body. The fasciculi arise from a fibro-tendinous strand which is attached behind to a superficial raphe which crosses the other three parts from the gape to the Q-M. joint, and, passing forward subdermally parallel with the outer edge of the teeth, is attached to Meckel's cartilage

at the symphysis. From this origin the fibres pass, with an inclination towards the symphysis, to the distant edge of the cartilage. In short, this muscle lies in contact with the outer surface of Meckel's cartilage in front of the angle of the mouth.

All these four parts are, in the majority of instances, fused more or less intimately along their contactual surfaces. They are all posterior to the mandibular ramus of the Vth nerve.

This quadripartite condition of the quadrato-mandibularis muscle is found not alone in the selachians, but also in the batoid elasmobranchs and in the heterodontids.

The significance of these parts will be discussed in the review and summary of the Elasmobranchs as a whole. I proceed to describe the quadrato-mandibularis as it was found in the forms dissected.

Chiloscyllium (Fig. 6).—Pars anterior (Qm.a.). This has a fibro-tendinous origin from the anterior edge of the quadrate portion of the palatoquadrate. The fibres curve cephalad and ventrad, and then ventrad, mediad and caudad to an insertion along the anterior one-half of the ventral edge of the expanded part of Meckel's cartilage.

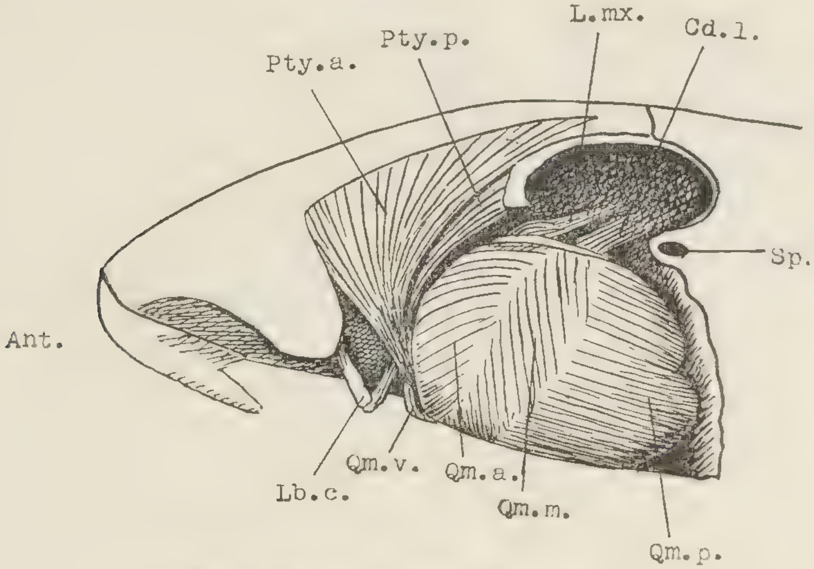


Fig. 6.—Mandibular muscles of *Chiloscyllium*.

The pars medialis (Qm.m.) is represented by a vertically disposed group of fasciculi whose surface appears as a narrow band of muscle behind the pars anterior, and whose fibres have a general direction ventrad and caudad, taking origin from a superficial fascia and passing deeply under the pars posterior behind. The upper fibres are inserted into the anterior surface of the muscular ridge along the posterior border of Meckel's cartilage. Those arising lower down are either blended with the pars posterior or inserted into the expanded portion of Meckel's cartilage in front of the muscular ridge.

The pars posterior (Qm.p.) arises from the greater part of the lateral surface of the expanded quadrate. The whole of the superficial fibres have a direction nearly horizontally caudad across the outer surface of the muscle, the lower portions of these horizontal fibres arise from the pars medialis. At the posterior border of the muscle these fibres all turn mediad and ventrad, and are inserted onto the posterior surface of the muscular ridge at the posterior end of Meckel's cartilage. The great bulk of the fibres, arising more deeply, pass ventrad and slightly caudad to be inserted onto the outer surface of the expanded portion of Meckel's cartilage between the ridge and the pars anterior.

The pars ventralis (Qm.v.) is quite small. It arises by a short tendon from the lower edge of the palatoquadrate and the subdermal tissues at the angle of the mouth, just in front of the tendon of the pterygoideus, and passing ventrad, mediad, and caudad, it crosses the mandible and the pterygoideus tendon, to be inserted on the mandible just behind the insertion of the tendon.

Pristiophorus (Fig. 5).—The pars medialis (Qm.m.) arises from the inner surface of the backwardly-projecting antorbital process and from a strong superficial aponeurosis which is attached to the upper margin of that process behind the orbit. The fibres pass cephalad, mediad, and ventrad, to mingle indistinguishably with those of the underlying pars anterior.

The pars anterior (Qm.a.) arises from the lateral surface of the palatoquadrate as far forward as the subocular muscular process. In this origin it covers the whole of the lateral surface of the palatoquadrate below the spiracle, except the narrow inferior strip against which the tendon of the pterygoideus lies. The insertion of these fibres is onto the lateral surface of Meckel's cartilage behind the angle of the gape.

The pars posterior (Qm.p.) is not defined from the posterior portion of the pars anterior; it arises from the quadrate portion of the palatoquadrate. Its fibres have a direction caudad and ventrad, to be inserted onto the lateral surface and posterior edge of Meckel's cartilage. The fibres having the latter insertion may be traced from their origin, which is along the dorsal edge of the quadrate.

These three portions are so intimately blended that it was only the directional differences of their fibres that enabled one to determine that the compact mass presented the usual divisions.

The pars ventralis is represented by a few fasciculi which arise from the anterior edge of the tendon of the pterygoideus below the angle of the mouth, and pass to be inserted on the inferior edge of Meckel's cartilage just in front of the insertion of the tendon.

In *Sphyrna* (Fig. 4) and in *Mustelus* (Fig. 8) the obvious division is into partes anterior and ventralis. When, however, the compact mass, which is apparently divided into upper and lower portions by the superficial raphe (R), is detached and studied from the deeper surface, directional differences corresponding to the four usual divisions become apparent. In both of these forms it is the pars medialis which is least definable.

Acanthias (Fig. 7).—This form was described by Marion and by him compared, not only with those described by Vetter, but also with *Raja*. If *Acanthias vulgaris* is similar to the species I have dissected, it would appear that Marion failed to dissect and study the adductor muscles from their deep surface, for his description is at variance with the conditions as I find them in certain particulars.

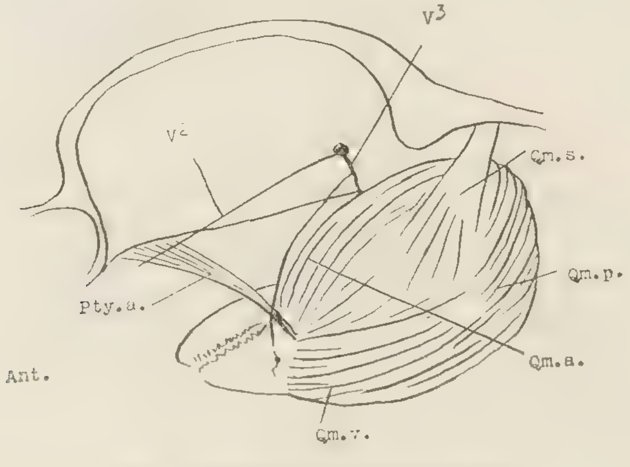


Fig. 7.—Mandibular muscles of *Acanthias*.

Pars medialis (Qm.m.) is a relatively small portion of the muscle which takes its origin from the very strong aponeurosis which covers the surface of the muscle in its upper portion. The aponeurosis itself is bound to the inferior margin of the spiracle and to the postorbital process. The direction of the upper and more superficial fibres is caudad and ventrad to an insertion on the posterior, and superficial, edge of the lower jaw below the Q-M. joint. The lower and more anterior fibres pass more directly ventrad and deeply, to blend with the partes anterior and posterior and to be inserted in the lateral surface of Meckel's cartilage.

Pars posterior (Qm.p.) takes origin from the lateral surface of the quadrate and from the posterior surface of its muscular process. The fibres take a curved course around the upper and under the ventral, superficial, portion of the pars medialis. Their direction is first ventrad and caudad, then ventrad, and finally cephalad. This direction is taken more by the fibres which arise from the posterior surface of the muscular process and from the upper area of the lateral surface of the quadrate, the deeper fibres passing more directly to the insertion. All the fibres are inserted on the lateral surface of Meckel's cartilage in front of the posterior insertion of the pars medialis.

The pars anterior (Qm.a.) arises from the anterior surface of the muscular process of the palatoquadrate. The fibres curve in the opposite direction to the superficial fibres of the pars posterior and the two have the mass of the pars medialis between them. Deeply the muscle blends with the partes medialis and ventralis, so that its insertion is inseparable from them.

The pars ventralis (Qm.v.) arises in part from the tendon of the pterygoid and in part from the strong fibrous tissues at and near the angle of the gape ; also it may be said to arise from or become the deep, insertional, continuation of the partes anterior and medialis. Omitting the fibres thus blended with those parts, the insertion of those having independent origin is onto the outer surface of Meckel's cartilage. Their direction is from origin mediad and cephalad.

The forward bulging of the anterior edge of the pars anterior and the blending thereof with the upper surface of this pars ventralis has resulted in the complete submergence of the tendon of the pterygoideus. In fresh specimens with quite soft muscles it was found, however, that almost the whole length of the tendon could be brought into view without actually detaching any muscle fibres from origin or insertion.

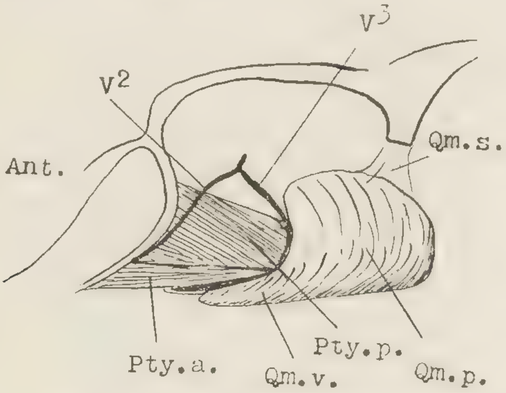


Fig. 8.—Mandibular muscles of *Mustelus*.

The motor nerve to the quadrato-mandibularis separates from the rest of the mandibular ramus of the Vth soon after that issues from the cranium. The main nerve then crosses the floor of the orbit and reaches the median border of the pars anterior of the quadrato-mandibularis and runs forward and laterad under the " overhang " of that muscle. At the angle of the mouth it crosses the tendon of the pterygoideus and turns mediad, caudad, and superficiad. The nerve to the quadrato-mandibularis crosses the orbit behind the main ramus, and disappears under the pars anterior at the base of the muscular process. It extends some distance into the muscle before breaking up into its numerous branches. There is a definite line of cleavage between the pars anterior and the muscle behind it which is occupied by the undivided motor nerve before it breaks up.

Marion's description mentions the origin of the pars medialis and the " broad thin sheet of fibres " related to it. He indicates the pars ventralis with the letter " x ", but fails to describe its relations to the other portions correctly or fully. Vetter's description (1874) is more precise. He correctly describes and figures the pars medialis and figures the superficial portion of it (Add. γ).

Heptanchus was described by Vetter (1874) and one may recognize in his description and figures that all four parts of the quadrato-mandibularis are present in that form. His Figure 1 quite clearly shows partes medialis (Add. γ) and ventralis, and the blended partes anterior and posterior.

2. **Heterodontus** (Figs. 9–14).

I have had for dissection five large specimens of *H. portus-jacksoni*, for which my thanks are due to the Director of New South Wales Fisheries Department.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Constrictors. (Figs. 9, 10.)

A. Dorsal.—These are completely similar to the partes inscriptionalis and arcuata of the dorsal superficial hyoid constrictor, which will be described later.

B. Ventral.—Each of these may be regarded as taking origin at the mid-lateral line, where it is uninterruptedly continuous with the corresponding dorsal constrictor. The fibres pass ventrad and mediad. Those of the pars arcuata become bound to the outer end of the ventral extrabranchial cartilage as they cross ventral to it; they then turn caudad slightly and become inserted onto the perichondrium of the coracoid between the insertion of the coracohyoideus and pectoral muscles. The fibres of the pars inscriptionalis also turn caudad and mediad ventral to the floor of the gill pouch. These are inserted into the aponeurosis of the coracomandibularis near its insertion onto the coracoid. These fibres of Csv.3 fuse with fibres of the pars arcuata of Csv.2. Fibres in front of these, that is, deeper into the gill pouch, which turn forward and are inserted into the extrabranchial cartilage are portion of the interbranchial muscle, for, if they be followed up into the vault of the pouch, it will be found that they are attached to the dorsal extrabranchial deep to the decussion with the Csv.2. Csv.4, 5 and 6 differ from Csv.3 only in that the ventral insertion is entirely into the coracoid.

HETERODONTUS.

——		Branchial Segment.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors.	Dorsal	Csd.3–6	Csd.2a and Csd.2b	Absent.
	Ventral	Csv.3–6	Csv.2a and Csv.2b	Csv.1a and Csv.1b
Deep Constrictors.	Dorsal	Cpr.3–6	Csd.2 pars profunda (C.pr.2)	Levator maxillae
	Ventral	Absent	Interhyoideus	Absent
Levators		Absent	Lev.2	Absent
Epibranchial Spinal Muscles		3–6	Absent	Absent
Adductors.	Dorsal	Ep.Ob.3–6	Absent	Pterygoideus
	Middle	Add.arc.br.3–6	Retractor mandibulae (add.hy.)	Quadrato-mandibularis
	Ventral	Absent	Absent	Absent
Depressors		Co.br.3–6	Coraco-hyoideus	Absent
Hypobranchial Spinal Muscles				

The Deep Constrictors. (Fig. 10.)

A. Dorsal.—The first interbranchial muscle, Cd.3.pr., third deep constrictor, takes origin above from the first dorsal extrabranchial cartilage. It is a thin sheet of fibres which lies against the anterior surface of the deep ends of the gill rays. The fibres run an arcuate course from origin to insertion onto the inferior extrabranchial cartilage. For the most part the fibres run parallel with the contiguous margin of Cs.3. Both above and below there is a small quadrate area of the muscle whose fibres are attached to the epibranchial and ceratobranchial cartilages respectively. These are parallel with those of the rest of the muscle, so that the effect produced is as though the acute angle these two cartilages make, one with the other, had invaded the interbranchial muscle and interrupted the continuity of the deep portion.

The remaining interbranchial muscles are essentially similar. The last two present similar relations but with absence of the extrabranchial cartilages.

There are no ventral deep constrictors in any of the branchial segments.

THE LEVATORS.

Whilst there are no levators, the arrangement of the deepest part of the deep constrictor is such that it is capable of acting as a levator. The superficial dorsal constrictors take their origin from very strong fine strands of fibrous tissue which in turn take origin from the septum between dorsal and ventral trunk muscles. The dorsal trunk muscles are considerably more massive than the ventral; the origin of the superficial dorsal constrictors is from the ventro-lateral aspect of the trunk muscle mass, close above the vaults of the gill pouches. The inner ends of the dorsal extrabranchial cartilages, from which, in other elasmobranchs, the levator muscles largely take origin, are bound to the ventral surface of the tendinous origins of the dorsal constrictors, and thus each is brought quite close to the dorsum of its respective arch. Just distal to the inner end of each extrabranchial cartilage we find a small quadrate piece of the deep constrictor which, taking origin from the extrabranchial, is inserted onto the epibranchial cartilage (Fig. 10).

Whether this piece of the deep constrictor is capable of acting independently cannot be stated, but it is fairly obvious that under such circumstances it would act as a levator, and we may, therefore, regard it as demonstrating a stage in the evolution of the levator muscles from the deeper portion of the deep constrictor sheet.

EPIBRANCHIAL SPINAL MUSCLES.

Each of these four muscles takes its origin from the outer, dorsal, surface of a pharyngobranchial cartilage near its postero-lateral margin. From this origin the fibres pass cephalad, covering the greater part of the surface of the cartilage of origin, and converge somewhat to be inserted onto the deep surface of the pharyngobranchial cartilage in front (Fig. 11).

THE ADDUCTOR MUSCLES.

A. Dorsal.—There are four oblique epiarcual muscles, which lie in the angles between the pharyngo- and epibranchial cartilages. Each takes origin from the proximal end of the pharyngobranchial and is inserted along nearly the full length of the posterior edge of the epibranchial cartilage of the same arch (Fig. 11).

B. Middle.—Each of the four adductores arcuum branchialium takes origin from a short length of the epibranchial cartilage close to the middle joint of the arch, and is inserted in a similar length of the ceratobranchial cartilage (Fig. 11).

There are no ventral adductors nor are there are ventral interarcual muscles in any of the branchial segments.

THE DEPRESSOR MUSCLES.

The coracobranchialis muscle is described in connection with the hypobranchial spinal muscles (Figs. 12, 13).

THE HYPOBRANCHIAL SPINAL MUSCLES.

When the ventral superficial constrictors and the deep hyoid constrictors are removed, the only muscle which is brought into view is the coraco-mandibularis. This is a relatively thick muscle which rises from a crescentic area on each side of the ventral surface of the coracoid and, narrowing as it extends forward, is inserted into the angle between the lower jaws (C-g., Figs. 12, 13). If this be detached in front, and on one side behind, and thrown back and to one side, practically the whole of the muscles rising from the coracoid will be brought into view.

The anterior coraco-branchialis rises from the deep aponeurosis of the coraco-mandibularis on either side of the midline immediately in front of the coracoid. The muscle is inserted alongside of its fellow of the other side, onto the junction of the hypohyal and first hypobranchial cartilage. There is no attachment to the floor of the pericardium, the insertion being well forward of the anterior limit of that cavity.

This muscle may be the "coraco arcualis communis" of Marion's descriptions; it is, however, absolutely in series with the other coraco-branchial muscles lying between the two coraco-hyoideus muscles and beneath the coraco-mandibularis. Were it not for the fact that it is completely separated from the rest of the muscles, doubt as to its complete serial homology would not arise.

The coraco-hyoideus muscle (C-h.) arises from the coracoid beneath the outer half of the area of origin of the coraco-mandibularis on each side; just anterior to its origin the muscle passes in contact with the lower end of the first extrabranchial cartilage and is firmly bound thereto, and receives fibres from the first interbranchial muscle which also is inserted onto that cartilage. The muscle extends mediad, cephalad, and dorsad, beneath the edge of the coraco-mandibularis, with the anterior coraco-branchial muscles lying medial to it for about half its length, and its fellow of the opposite side in front of them. It is inserted onto the ventral face of the medial end of the cerato-hyal cartilage.

The coraco-branchial muscles rise from the antero-ventral edge of the coracoid along the boundary of the pericardium. The inseparable posterior components are inserted onto the ventral surface of the cardio-branchial along the lateral and antero-lateral border. The remaining members of the set are inserted onto the ventral surface of the first three hypobranchials.

THE MUSCLES OF THE HYOID SEGMENTS.

The Superficial Constrictors.

A. Dorsal (Fig. 9).—There is an intimate fusion between the successive superficial constrictors of the branchial region, especially so dorsally.

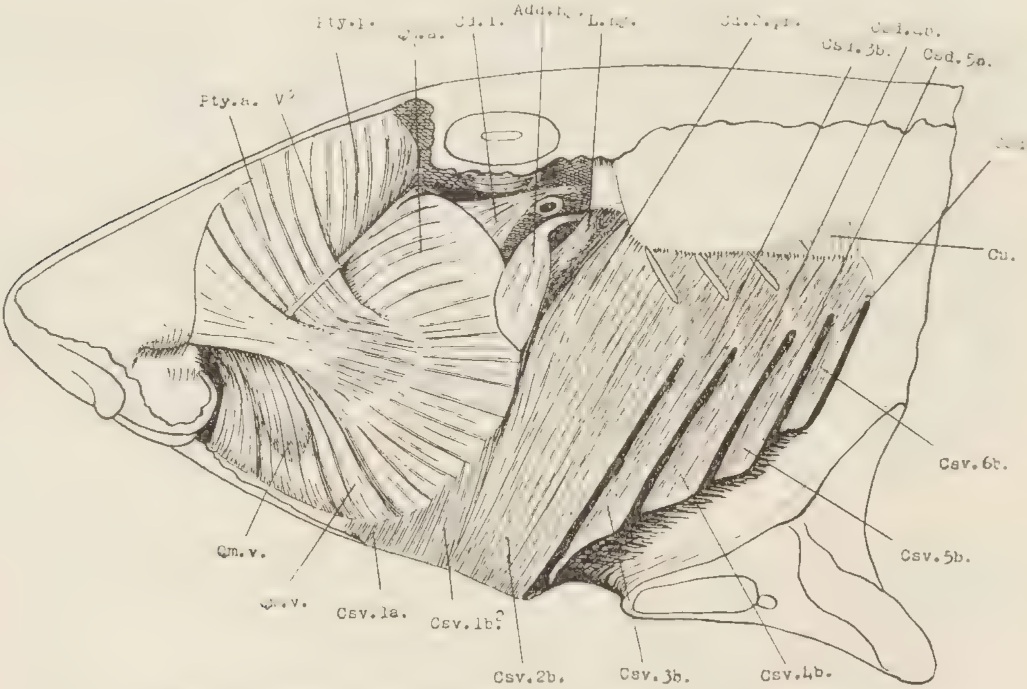


Fig. 9.—*Heterodontus portusjacksoni.* Lateral view of a superficial dissection.

The first of these is the hyoid (Csd.2). This takes origin from the hyoid levator and from the aponeurosis of the lateral trunk muscles. The most anterior fibres, those arising from the levator hyoidei, are deeply placed and lie against the pseudo hyoid cartilage from which the hyoid gill rays spring. Those immediately behind these lie more superficially against, anterior to, the deep portions of those gill rays. These fibres arise from the fascia dorsalis and are uninterrupted throughout their length. The fibres behind these, lying against the outer ends of the gill rays, are interrupted at the first dorsal extrabranchial cartilage. This lies oblique to the axis of the body above the first gill pouch at the confluence of the anterior (superficial) and posterior (deep) walls. The fibres of Csd.2 which we are dealing with take origin quite deeply from the aponeurosis of the trunk muscles above, behind and medially to the extrabranchial cartilage. Their direction from their origin is laterad and slightly cephalad and ventrad, and they are inserted into the perichondrium of the cartilage. From the other side of the cartilage two other sheets of muscle fasciculi take origin, a superficial and a deep sheet. The superficial sheet consists of the fibres of the Csd.2 which lie against the outer ends of the hyoid gill rays. The deep fibres are portion of the first interbranchial muscle, Cd.3.pr. The last and most posterior series of fibres of Csd.2 is completely mingled with Csd.3 fibres at their origin. They arise in part from the fascia dorsalis, aponeuroses of the trunk muscles, and in part from the lower edge of the second dorsal extrabranchial cartilage. They pass down in the anterior wall of the first gill pouch between the outer ends of the gill rays and the edge of the gill cleft. Unlike the last series of fibres these are not interrupted by the first dorsal extrabranchial cartilage. On the other hand, the continuation of the line of that cartilage corresponds to the dorsal fornix of the gill pouch and ends at the top of the cleft, and here there is a division into two sheets of fasciculi, a superficial and a deep, just as was found further forward. The superficial sheet is composed of the posterior series of Csd.2, the deep sheet of the anterior series of Csd.3 (the pars inscriptionalis); these lie in the posterior wall of the first pouch under cover of the anterior wall.

The first portion of Csd.2 is to be regarded as serially homologous with the interbranchial muscles and will be designated the second deep constrictor, Cd.2.pr. It lies against the arcuate pseudo-hyal cartilage and the deep ends of the gill rays, and its fibres are not interrupted by the extrabranchial cartilage. The second portion we will designate the pars inscriptionalis, Csd.2a, the third will be the pars arcuata, Csd.2b.

These last two designations are, of course, adopted from Lightoller, but if confusion is to be avoided it must be clearly realized that his Csd.2b and Csd.2c correspond to my Csd.2a and Csd2b, and Lightoller's "pars epiphyoidea, Csd.2a" to my Cd.2.pr.

Each of the remaining superficial dorsal constrictors presents portions which correspond absolutely to Csd.2a and Csd.2b, and may be described in all their relations to the successive dorsal extrabranchial cartilages and gill pouches by simply changing the numbers in each case. There are, however, no extrabranchial cartilages in the superior fornices of the last two pouches—slight tendinous interruptions take their places.

B. Ventral.—The superficial ventral hyoid constrictor presents features not found in any other elasmobranch. The muscle takes origin from the ventral median raphe. The pars arcuata arises superficially behind the extramandibularis portion of Csv.1, the pars inscriptionalis takes origin under cover of that same portion of Csv.1. The fibres of the pars arcuata are parallel with those of Csv.1 but those of the pars inscriptionalis incline forward, crossing the more superficial fasciculi at an acute angle. This difference of direction permits of the separation of the two muscles, but only by the most careful dissection, for they are very closely bound together. The fasciculi of the pars inscriptionalis are inserted into the posterior edge of the lower jaw under cover of the posterior fibres of the pars extramandibularis of Csv.1; this insertion is by a strand of fibrous tissue to which the muscle fasciculi converge. The pars arcuata is continued dorsally into the pars arcuata of Csd.2.

The Deep Hyoid Constrictors.

A. Dorsal.—This muscle has been described in connection with the Csd.2.

B. Ventral.—The interhyoideus muscle takes origin from the ventral median raphe under cover of the intermandibularis portion of Csv.1; this origin extends from the anterior limit of the origin of Csv.2a almost to the symphysis. The muscle is fan-shaped, the fibres converging to be inserted onto the ventral edge of the ceratohyal not far from the joint with the epihyal and just medial to the median end of the pseudohyal cartilage. The posterior margin is, for most of its length, in contact with the anterior margin of Csv.2a.

The relations of the two portions of the hyoid superficial constrictor to one another and to the deep constrictor, and the relations of all three to the mandibular ventral constrictor in *Heterodontus* present quite accurately that primitive arrangement of the constrictor sheets which is observed throughout the elasmobranchs in the arrangement of the dorsal homologues in the branchial segments.

The Hyoid Levator. (Fig. 9, Lev.hy.)*

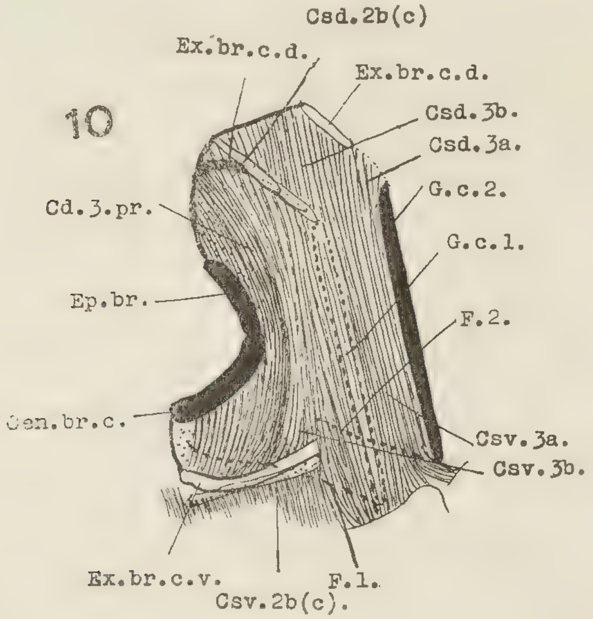
The very primitive hyoid levator has its origin from the auditory capsule. This origin is, without any tendinous assistance, from the lateral ridge of the capsule above the attachment of the oto-hyoid ligament. The fibres pass ventrad, laterad, and cephalad, to be inserted directly into the hyomandibular cartilage behind and deep to the belly of the adductor hyoidei muscle.

---

* Lightoller (1939) has designated this muscle pars nucho-maxillaris of the first (mandibular) dorsal constrictor; it is the Csd.1c of his description.

The Hyoid Adductor. (Fig. 9, Add.hy.)

B. Middle.—The adductor hyoidei is that muscle which, in some other elasmobranchs, has been termed retractor mandibulae. In common with the branchial adductors it takes its origin from the anterior edge of the epiarcual element, hyomandibular. The origin extends onto the lateral surface of the cartilage. Some of its more superficial, and posterior, fibres take origin


10
Csd.2b(c)
Ex.br.c.d.
Ex.br.c.d.
Csd.3b.
Csd.3a.
G.c.2.
Cd.3.pr.
G.c.1.
Ep.br.
F.2.
Gen.br.c.
Csv.3a.
Csv.3b.
Ex.br.c.v.
F.1.
Csv.2b(c).

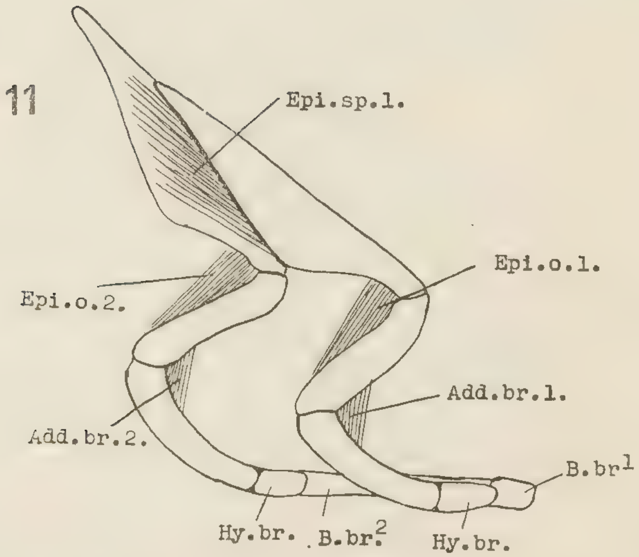

11
Epi.sp.1.
Epi.o.1.
Epi.o.2.
Add.br.1.
Add.br.2.
B.br1
Hy.br.
B.br2
Hy.br.

Fig. 10.—*Heterodontus.* The anterior view of the posterior wall of the first gill pouch. The hyoid constrictor sheet has been dissected off, and the muscles which lie in the floor of the gill pouch, and which turn mediad almost at right angles to the plane of the rest, have been represented as turned down into the same plane.

Fig. 11.—*Heterodontus.* Two branchial arches.

from the very strong oto-hyoid ligament, which, firmly attached to the hyomandibular above and behind the muscle, passes to the lateral ridge of the auditory capsule just above the incisura venae capitis lateralis. From this origin the fibres pass laterad, cephalad, and ventrad to a fleshy insertion onto the capsule of the Q-M. joint.

Innervation.—This is by a twig from the hyomandibular ramus of the VIIth nerve.

There is no ventral adductor and no ventral interarcual muscle in the hyoid segment, and the coraco-hyoideus has been described along with the hypobranchial spinal muscles.

THE MUSCLES OF THE MANDIBULAR SEGMENT. (Figs. 9, 14.)

The Superficial Constrictors.

A. Dorsal.—Immediately in front of the spiracle on removal of the skin, one displays the outer edge of a muscle whose anterior surface lies more deeply. This, which is regarded as representing the whole of the derivatives of the dorsal constrictor sheet of the mandibular segment, takes origin from a short line immediately above and internal to the oto-hyoid ligament. From this origin the muscle passes laterad, cephalad and ventrad to a much wider insertion onto the dorsal edge of the palatoquadrate. The superficial fibres pass most directly laterad, and the deepest have the greatest inclination cephalad.

The superficial portion of this muscle is, it is believed, unquestionably the primitive constrictor sheet. The deeper portion corresponds just as unquestionably to the mandibular levator of the selachians.

In all the segments behind, it has been observed that the deep constrictor (and its dorsal and deeper portion which is apparently capable of acting as a levator) form one continuous sheet.

Here again, then, it appears that *Heterodontus* presents the retention of primitive features. Whilst it is quite impossible to define the muscles, it is probable that this, which we designate Cd.1, truly represents also those other muscles.

B. Ventral.—The Csv.1 muscle presents, on either side of the median ventral raphe, no division into a and b but, on the other hand, the anterior portion is inserted into the ventral and median edge of the lower jaw, whilst approximately the posterior half is inserted into a strong fascia which is continued up and over the surface of the jaw. Partes inter- and extra-mandibularis are therefore recognizable, and definable by the insertion (Csv.1a, Csv.1b^2).

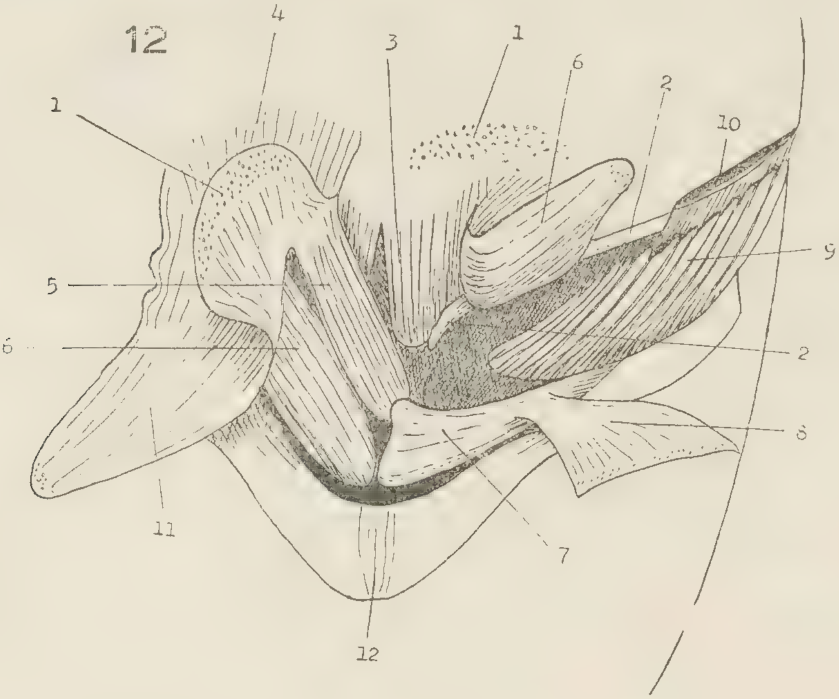
The Mandibular Adductors. (Figs. 9, 14.)

The adductor mass of *Heterodontus* is particularly complex and it was at first thought that the mass included both superficial and deep constrictor components. Later comparisons with the adductor masses of the various selachian and batoid forms which I have been enabled to dissect have convinced me that there are representatives of the dorsal and middle adductors only. Comparison is invited particularly with the adductor muscles of *Mustelus*, *Acanthias* and especially *Chiloscyllium*, which present two degrees of complexity, whilst *Heterodontus* is regarded as presenting a third, more complex than the last. In considering the interpretation to be placed upon the parts of this muscle, it is necessary to keep in mind the fact that the palatoquadrate has been brought into much closer union with the base of the skull than in any of the selachian or batoid elasmobranchs. This close approximation and union has permitted the transfer of muscular origins to skull areas which were not mechanically suitable in the other forms. Not only is this so, but the extraordinary increase in size of the palatoquadrate and its very close union with the skull below and in front of the orbit has covered those areas whereto muscles are attached in the selachians, and, as it were, necessitated new origins for these muscles.

The pars anterior of the pterygoideus (Pty.a.) (epiarcual oblique mandibular or dorsal adductor muscle) takes origin from the posterior subdermal edge of the nasal capsule and from the subdermal edge of the cranium for a short distance behind the capsule. Its fibres converge to a relatively broad flat tendon which does not burrow into the adductor mandibulae but becomes continuous with the superficial aponeurosis of the adductor. As in the selachians, this muscle is crossed by the superior maxillary branch of the fifth nerve between its origin and insertion.

The pars posterior (Pty.p.) arises more deeply, under cover of the pars anterior, from the side wall of the cranium, its origin extending back almost to the anterior margin of the orbit. Anteriorly it arises from the inner portion of the posterior wall of the nasal capsule. It has the superior labial cartilage imbedded in its deeper and anterior part, and some of its fasciculi take origin from the tough investment of the cartilage. Its deep surface is incompletely covered by a tough fibrous membrane which is loosely attached to the submucous tissues of the wall of the mouth between the jaws. Its fasciculi pass almost directly ventrad to be inserted into the upper edge of the lower jaw and the tissues of the side wall of the mouth just behind the angle of the gape. The posterior deep edge of the muscle is clothed by a strong tendon into which the bulk of its fibres are inserted, and it is this tendon particularly which is inserted onto Meckel's cartilage.

12



13

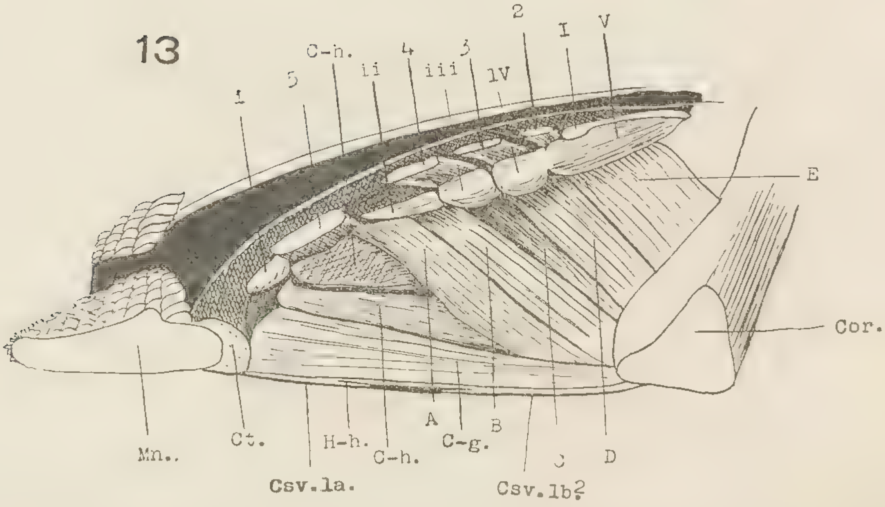


Fig. 12.—*Heterodontus*. A deep dissection of the floor of the mouth, seen from below. 1. Right head of the m. coraco-mandibularis, cut free and turned back. 2. First ventral interbranchial cartilage. 3. M. coraco-branchialis. 4. Left head of the m. coraco-mandibularis. 5. First slip of the m. coraco-branchialis. 6. M. coraco-hyoideus. 7. Ceratohyoid cartilage. 8. M. interhyoideus, cut free from the mid-line and folded back. 9. Hyoidean and pseudohyoidean gill rays. 10. First gill slit. 11. Body of the m. coraco-mandibularis cut free from the symphysis and pulled to one side. 12. Symphysis of the lower jaw.

Fig. 13.—*Heterodontus*. A dissection of the coraco-branchial and coraco-mandibular muscles seen from the mid-line. I-V, the basibranchial cartilages. A, B, C, D & E, the several slips of the m. coraco-branchialis.

Innervation.—This is by two branches from the mandibular ramus of the Vth nerve which leave the main nerve before it crosses the anterior inferior border of the orbit.

There is a little doubt as to whether it is the more superficial or the deeper part of this muscle which truly represents the pars anterior of the typical selachian muscle.

The mandibular ramus of the Vth nerve issues from the orbit along a deep fissure between the pars posterior of the pterygoideus and the pars anterior of the quadrato-mandibularis. After giving off the motor twigs to the quadrato-mandibularis, the nerve turns superficiad and crosses the tendon of the pars anterior of the pterygoideus.

As in the selachians, except just before their insertion onto Meckel's cartilage, there is no fusion between the contactual surfaces of the pterygoideus and the pars anterior of the quadrato-mandibularis.

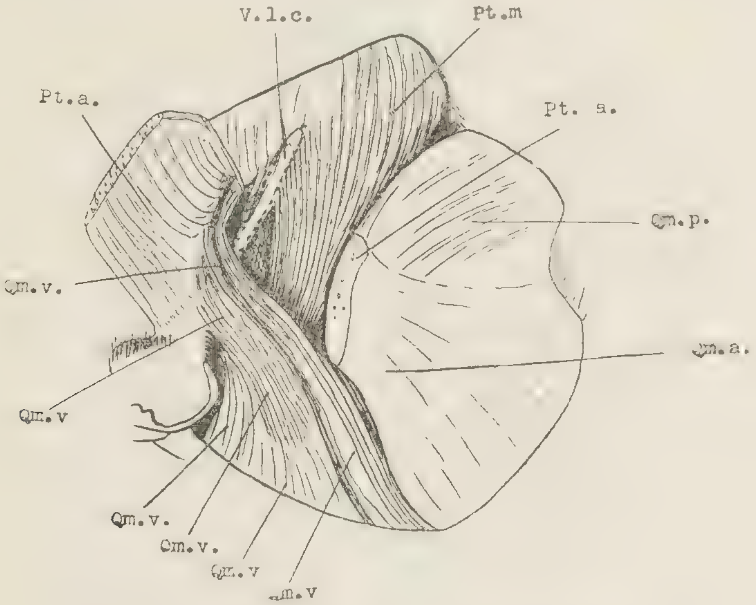


Fig. 14.—*Heterodontus.* A deep dissection of the mandibular muscles.

THE QUADRATO-MANDIBULARIS MUSCLE. (Figs. 9, 14.)

Pars medialis.—This portion of the muscle has largely lost its identity. The surface of the main mass is invested in a very strong superficial aponeurosis which, instead of being continued up onto the antorbital process, is firmly attached above to the superficial edge of the arch of the palatoquadrate below the posterior half of the orbit. This gives origin to a considerable proportion of the fasciculi of the muscle, and is to be regarded as representing the pars medialis.

Pars anterior (Qm.a.).—From the arch of the palatoquadrate below the anterior half of the orbit, a mass of thick fasciculi take origin and swing cephalad and ventrad, and then ventrad and caudad, to be inserted into Meckel's cartilage immediately behind the pars medialis of the pterygoideus. These clearly constitute the pars anterior of the muscle.

Pars posterior (Qm.p.). -The fibres arise from the palatoquadrate under cover of, and are immediately blended with, the medialis and pass ventrad to be inserted into the expanded posterior part of Meckel's cartilage.

The pars ventralis (Qm.v.) fibres arise from the deep tissues of the inner wall of the mouth around the gape and behind the fold of the lower lip. They are inserted onto the outer surface of Meckel's cartilage in front of the insertion of all the other portions. Some of the fibres of this part arise from the deep surface of the tendon of the pars anterior of the pterygoideus; they are the longest and most posterior fasciculi of the muscle, and their insertion is posterior and superficial to the tendinous insertion of the pars posterior of the pterygoideus.

The extent of fusion of the deep fibres of the pars anterior and the posterior fibres of the pars ventralis with the pterygoideus muscle is rather in excess of the normal as presented by the selachians generally, but not greatly in excess of the fusion in such a form as *Pristiophorus.*

3. The Batoidei.*

I have had for dissection one very large specimen of *Dasyatis brevicaudatus* Hutton, one specimen of *Raja australis* Macleay, three specimens of *Urolophus testaceus* Mull. & Henl., one specimen of *Hypnarce subnigra* Dumeril, and one of *Taeniura lymna*. For the specimens of *Raja* and *Taeniura* I have to thank the Trustees of the Australian Museum and the former Director, Dr. C. Anderson. For the others I have to thank various fishermen friends.

The *Dasyatis* was the first dissected and described, *Raja* being compared with it at each stage of the dissection. These two are, therefore, described at length. Such differences as called for note, observed in the dissection of the other forms, are recorded later.

I would at the outset draw attention to the discovery of two veritable glosso-pharyngeal muscles innervated by the facial nerve in *Dasyatis*. It is not proposed to anticipate a later section by discussing their bearing on the evolution of the cranio-glossal and hyo-glossal muscles

THE BATOIDEI.

Raja (R.) and *Dasyatis* (D.).

——		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors.	Dorsal ..	Csd.3–6. R.D.	Csd.2b. Levator rostri. R.D. Csd.2c. R.D.	Absent
	Ventral ..	Csv.3–6. R.D.	Csv.2b. depr. rostri. R.D. Csv.2c. R.D.	Csv.1a and Csv.1b
Deep Constrictors.	Dorsal ..	C.pr.3–6. R.D.	C.pr.2. R.D.	Lev. max. sup.
	Ventral ..	Sub.arc.tr.3–5. R.D.	Interhyoideus. R.D.	Lev. palati
Levators		Lev.3–6. R.D.	Lev.2. R.D.	Absent
Epibranchial Spinal .. Muscles.		3–6. R.D.	Absent	Absent
Adductors.	Dorsal ..	Ep.ob.3–6. R.D.	Ep.ob.2. Lev.hyo-mandib. R.D.	Pterygoideus
	Middle ..	Add.arc.br.3–6. R.D.	Cranio-glossus. D. Absent. R.	Quadrato-mandibularis
	Ventral ..	Absent. R.D.	Hyoglossus. R.D.	Absent
Depressors		Co.br.3–6. R.D.	Co-hy.	Absent
Not accounted for		Nil	Nil	Mandibulo-labialis Maxillo-labialis
Hypobranchial				

---

* *Dasyatis* was the first of the large subjects that I stained prior to dissection. Some time previously, whilst at work on the development of the selachian muscles, it became necessary, in checking a dissection, to work on a specimen which had been stained with picrocarmine for sectioning purposes. It was found that the muscles and nerves had taken a macroscopic differential stain that made the dissection remarkably easy. This naturally led to the staining of all small specimens before dissection, and later to similar treatment of the larger subjects. The ease and confidence with which one can follow the finer nerve twigs after the staining needs to be experienced to be realized. The staining proceeds much more rapidly and satisfactorily after skinning, but if superficial nerves are to be studied the specimens should be stained for about a week before skinning. I use 50% alcohol saturated with picric acid and rendered alkaline with potash, and then add sufficient Grenacher's alcoholic borax carmine to give the solution a dark red colour. More carmine may need to be added as the specimen absorbs the colour. The use of the picric acid has the advantage of greatly deodorising the specimens, and the disadvantage of staining the fingers. But one early learns to put on one's gloves before handling the specimens. If the specimens have been long preserved and are darkened by age, the results are not so satisfactory. The carmine stain fails altogether, the picric acid alone is useful; it differentiates the nerves, but not nearly so well as in the fresh specimens. This staining is useful only if the muscles are white.

of higher vertebrae, but rather to invite a more critical examination of the interpretation of their serial homology with muscles of the branchial arches which is offered here.

In the Rays we find two muscles, undoubtedly hyoid, in front of the hyoid visceral cleft, the spiracle. In these fishes we have an undoubted division of the muscle sheet by the spiracle. It would seem, however, that the portion anterior to the spiracle has resulted from a secondary up-growth from the plate which, primitively, was situated behind the cleft after the closure of the ventral end thereof.

There is ample evidence of such a forward growth of the hyoid muscles in the history of the development of the Teleostomes, e.g. the adductor arcus palatins. We, therefore, explain these prespiracular hyoid muscles as much modified forms of the specialized deep muscles found in branchial arches.

As in the other subsections, I preface the description of the muscles by their tabulation.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Constrictor Muscles.

Dasyatis.—The dorsal and ventral constrictors are in series, one behind the other, presenting the appearance of a longitudinal muscle with a series of transverse tendinous intersections. The direction of the component fasciculi is antero-posterior with an inclination latero-caudad. On the dorsum the series is firmly attached medially to the fascia dorsalis, and is limited by that fascia. Inasmuch as the fasciculi strike that fascia with an inclination cephalad and mediad, the medial limiting fasciculi take origin from it. Laterally the dorsal constrictors appear to be limited by the fascia which binds the heads to the embracing propterygia. This, however, is not the fact. The dorsal perimysium, only, of each muscle is bound to that fascia, the muscle itself continuing uninterruptedly down the side of the head against the propterygium and its dorsal and ventral superficial tissues and muscles, until the ventral deep fascia is reached. Into this deep fascia the limiting fasciculi are inserted with a caudad and ventrad inclination. From the ventral and medial side of this limitation of the dorsal constrictors the fasciculi of the ventral constrictors take origin. There is a very definite, though narrow, tendinous interruption between the two sets of fibres along this line. But for this interruption the two muscles would be quite continuous, for their component fasciculi are absolutely parallel. Medially the ventral constrictors are inserted into the deep surface of the ventral deep fascia* beneath the depressor rostri in front and the tendon of the longitudinal muscles further back.

Each of the superficial constrictors* takes origin in front between its medial and lateral margins from a tendinous interruption in the interbranchial septum between it and the interbranchial muscle (deep constrictor) and is inserted into a similar interruption in the interbranchial muscle wall behind. It is the dip ventrad or dorsad to reach this interbranchial interruption which, superficially, presents the appearance of a tendinous interruption between the successive muscles.

The sixth dorsal superficial constrictor is inserted posteriorly into the fascia dorsalis and the deep tissues in front of the base of the propterygium.

The sixth ventral constrictor has a much more interesting insertion. The muscle disappears from superficial view beneath, i.e., dorsal to, the lateral edge of the coraco-arcualis communis. Under cover of this muscle it passes ventrally to the pars posterior of the coraco-branchialis, folds dorsad round the medial border thereof, and is inserted into the perimysium on its medial surface; this insertion is one of the factors which gave rise to the view expressed in the last footnote. We have here a superficial muscle, which must in the primitive condition have been inserted into the superficial fascia, presenting an insertion deep to the invading spinal muscles. The superficial fascia has been split into superficial layers along its length or divided across its length. There is no submergence of primitively superficial insertions in front of the hyoid segment.

The insertion of the sixth superficial constrictor superficial to the pars posterior of the coraco-branchialis, thus separating that muscle from the longitudinal spinal muscles, is just as one would anticipate in view of the development of the former from the ventral ends of the branchial muscle plates. Their situation and their development prove them to be deep branchial muscles.

---

* It is believed that the invasion of the cephalic region ventrally by the spino-occipital muscles was accompanied by a division of the deep fascia between the hyoid and branchial segments. The deep fascia being submerged behind the hyoid segment, but being superficial to the anterior attachments and prolongations of the spinal muscles at and in front of the hyoid segment.

Raja.—Marion (1905, p. 11) says that in *Raja erinacea* there are seven superficial constrictors. I can find no evidence of this in *R. australis*, and in this form the superficial constrictors resemble so closely those of *Dasyatis* that they do not call for separate description. An examination of Marion's figures and description leads one to the discovery that his seventh constrictor is obtained by the division of the hyoid sheet. Since there be no deep muscles to correspond with the extra superficial constrictor, nor, indeed, any branchial arch to account for the seventh, one must conclude that he was in error in his treatment of the hyoid sheet. *R. australis* presents no indication of any division of the superficial hyoid sheet.

THE DEEP CONSTRICTOR MUSCLES.

Dasyatis.—The anterior wall of the first gill pouch is provided with a deep constrictor by the hyoid muscle sheet. Behind this are four branchial deep constrictors. These four interbranchial muscles are so very similar that a description of one serves as a description of all.

The outline of each interbranchial wall is that of a truncated wedge with the truncated end outwards and with a triangular gap cut nearly symmetrically out of the centre of the broad end of the wedge. This gap is occupied by the pharyngeal passage and bounded by epi- and cerato-branchial cartilages. The wall is clothed, antero-laterally to the gill rays, by the interbranchial muscle. This is divided into dorsal and ventral halves by a horizontal tendinous interruption, which extends from the pharyngeal angle to the outer margin of the wall and is due to the insertion of the adjacent ends of the dorsal and ventral fasciculi into the perichondrium of a dominant middle gill ray. The direction of the fasciculi is dorso-ventral, but with a slight inclination mediad from the horizontal midline both above and below.

Raja.—I find the interbranchial muscles of *R. australis* to be essentially similar. The fasciculi radiate at the outer end precisely as Marion indicates. For illustrations of these muscles Marion's work may be consulted.

THE SUBARCUALIA TRANSVERSI.

Marion (p. 17), writing of the branchial interbranchial muscles of *Raja*, says: "A few bundles of the most median fibres of the ventral portions are overdeveloped, and have extended so as to take their origin from the fascia covering the coraco-mandibularis muscle. A similar condition was noted above for *Acanthias*, but these fibres were not as prominent there as here. Tiesing, basing his opinion on the work of Vetter upon *Heptanchus*, has regarded these fibres as a deeper layer of the constrictor, but *Acanthias* shows this not to be tenable. There is the resemblance to a constrictor", and yet on page 26 he writes: "It may be a question whether the interbranchiales, the interarcuales, and the adductors do not form a system of deep as opposed to the superficial constrictors".

To these muscles, which Tiesing designated Csvp.3-5, I propose to apply the designation subarcualia transversi.

I have found them in all the rays I have dissected. They are, as it were, foreshadowed in *Heterodontus* and the Selachii by an always small and varying bundle of ventro-median fasciculi of the deep constrictor sheets, which swings across toward or to the midline with the deepest fibres of the pars interinscriptionalis.

These muscles do not conform to the definition of subarcualia transversi given elsewhere, for they do not cross the midline to meet their antimeres. On the other hand, they certainly appear to present, as it were, an incomplete attempt to form such a muscle, and to that extent they foreshadow a modification of the subarcual muscles found constantly in the bony fishes.

THE LEVATORS ARCUUM BRANCHIALIUM.

Dasyatis. There are five branchial levators. Each consists of a dorsal and a ventral portion, separated by a relatively broad tendinous central area. These muscles lie in the medial wall of the gill pouches above the pharyngeal plane and against the capiti-nuchal muscles. Each takes origin from the fascia dorsalis beneath the median origin of the superficial dorsal constrictors. They lie in an antero-posterior vertical plane and the fasciculi have a dorso-ventral direction with a slight inclination caudad. The insertion is into the epibranchial cartilage lateral to the epiarcual obliqui muscles.

---

* It should be noted that there is in no one of these superficial constrictors any indication of divisibility into partes arcuata and inscriptionalis.

Raja.—The levators in this form would not be recognized as such had one not dissected the other form. They are found in the same situation in the two forms, but in *Raja* each muscle supplies a complete median wall to its pouch, and the fasciculi run in a cephalo-caudad direction with a slight inclination ventrad. They take origin from an interbranchial interruption in front, and from the fascia and the superficial constrictor above, and are inserted into the interbranchial interruption behind and the epibranchial cartilage.

Marion failed to describe these muscles in *R. erinacea.*

The Epibranchial Spinal Muscles.

Dasyatis.—These are essentially similar to those of *Heterodontus,* but are not as well developed; there are four, but there is no subspinalis.

Raja.—The muscles are, as Marion states, represented by fibrous bands, in which no muscle fibres can be detected.

The Adductor Muscles.

Dasyatis.—The epiarcualis obliqui and adductores arcuum branchialium are essentially similar to those of the Selachii.

Raja.—The muscles are essentially similar.

Ventral oblique muscles are developed in neither form.

The Depressores Arcuum Branchialium.

Dasyatis.—The coraco-branchialis muscle is divided into anterior and posterior portions which are not in contact with one another.

Pars anterior.—This consists of four small muscles which take origin together from the deep (dorsal) surface of the coraco-arcualis communis muscle well forward, close to the limit of its muscular portion.

From this origin these muscles pass dorsad, with an inclination cephalad, in front of the pericardium and in contact laterally with the expanded ends of the ventral extrabranchial cartilages. The muscles are quite inseparable either from one another or from the coraco-arcuales communes at their origin, but they taper to narrow tendinous insertions which are separated by the passage of the main branches of the ventral aorta. The insertions are onto the median ends of the cerato-branchial cartilages.

Pars posterior.—This massive muscle has an extensive origin from the lateral end and ascending portion of the coracoid arch lateral and dorsal to the lateral portion of the origin of the coraco-arcualis communis muscle. This area of origin extends dorsally on the anterior face of the pectoral girdle to the point of union of the fifth cerato-branchial cartilage with the arch, which is also the inferior limit of the insertion of the trapezius. From this origin the muscle passes cephalad and slightly mediad and dorsad along the posterior wall of the fifth branchial pouch, to be inserted along the length of the dorsal edge of the fifth cerato-branchial cartilage and the posterior edge of the fifth extrabranchial cartilage. Thick at its origin, the muscle is laterally flattened at its insertion.

Raja.—I find a very similar division of the muscle in *Raja.* Here, however, they might more descriptively be termed partes ventrales et dorsales. The anterior or ventral portion is continued back beneath the coraco-arcuales communes in contact with the posterior, or dorsal, part and terminates in a tendon which gives it origin from the coracoid arch beneath the lateral margin of, and independently of, the coraco-arcuales communes.

THE MUSCLES OF THE HYOID SEGMENT. (Figs. 15, 16.)

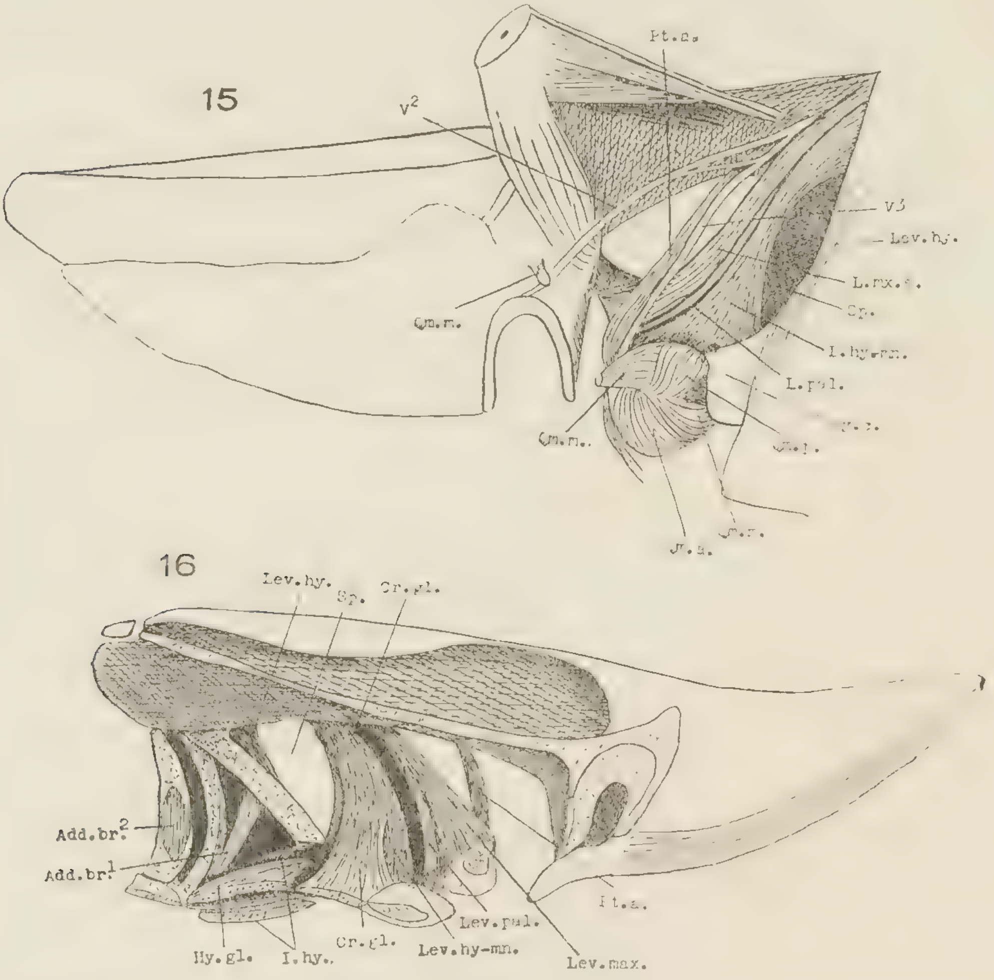
The Superficial Constrictor Muscles.

The form of the superficial and deep hyoid constrictors, and their relation to the gill pouch behind them, are, in their close resemblance to the homologous branchial muscles, particularly interesting and instructive.

Dasyatis.—The second superficial dorsal constrictor is not divisible in the Rays into partes arcuata et inscriptionalis. The fasciculi have a general direction from in front, caudad and laterad, parallel to those of the branchial constrictors behind them. The most anterior portion of the muscle is hidden from view, and here the fasciculi all take origin from a well-marked fascial band on the anterior wall of the first gill pouch. This band takes origin from the fascia dorsalis well towards the dorsal limit of the atrio-pharynx and passes horizontally laterad to be attached to the lateral gill-pouch wall. From this band the fasciculi first pass dorsad, and, becoming superficial, curve caudad and laterad as described, to be inserted into the first tendinous interruption, which latter is placed over the first interbranchial septum.

Raja.—The muscle in *R. australis* is almost entirely similar. As previously noted, Marion found here two superficial constrictors in *R. erinacea.*

The levator rostri, a muscle present in *Raja* but not in *Dasyatis,* is probably a specialized portion of the superficial hyoid constrictor. Marion's description of the muscle is correct in all particulars.



Figs. 15 & 16.—*Dasyatis.* Lateral and median view of some of the hyoid and mandibular muscles.

Dasyatis.—The superficial ventral hyoid constrictor is a sheet of muscle essentially similar to the branchial constrictors behind it. The more medial fibres are continuous with those of the first (hyoid) interbranchial muscle in front of and deep to it. The more lateral take origin in the connective tissues of the gill wall. The insertion of all is into the tendinous interruption beneath the first interbranchial septum.

The depressor rostri, which takes origin from the ventral deep fascia superficial to this last, is probably a specialized modification of this sheet.

Raja.—The muscles in *Raja* are essentially the same as in *Dasyatis.*

THE DEEP HYOID CONSTRICTOR MUSCLES.

Dasyatis.—The hyoid interbranchial muscle (Cd.2.pr.) in both *Dasyatis* and *Raja* are so completely similar to the branchial interbranchial muscles that they call for no further description.

The interhyoideus, which has been treated by previous writers as portion of the hyoid superficial constrictor, is essentially similar in the two forms. It is a fan-shaped muscle which takes origin in the ventral deep fascia superficial to the longitudinal ventral spinal muscles. From this relatively broad origin, the fasciculi converge to be inserted onto the posterior surface of the hyo-mandibular cartilage near the centre of its length by a short tendon which reaches nearly to the dorsal edge of the cartilage.

THE LEVATOR HYOIDEI.

Dasyatis and *Raja.*—This is a powerful muscle which has an extensive origin from the skull and fascia dorsalis, behind the auditory capsule and above the articulation of the hyo-mandibular cartilage to the skull. The muscle tapers rapidly and passes laterad, ventrad, and slightly cephalad, to be inserted onto the dorsal edge and anterior face of the hyo-mandibular cartilage extending a little more than half-way along the length on the dorsal edge.

THE ADDUCTOR MUSCLES. (Figs. 15, 16.)

In both *Dasyatis* and *Raja* and, in fact, in the other batoid forms dissected, the hyoid adductor is relatively a very extensively developed muscle. It is believed that there has been here a complete fusion of the adductor and the oblique epiarcual muscle, though it well may be that the whole muscle is the resultant of increase in function and, consequently, bulk of the adductor.

Dasyatis (Figs. 15, 16).—The adductor hyoidei in this form is a truly remarkable muscle, and for the purposes of a later section of this paper it will be described in two portions, an internal and an external, which will be designated "cranio-glossus" and "levator hyo-mandibularis" respectively.

Levator hyo-mandibularis (Lev.hy-mn.).—This is a very powerful muscle which takes origin behind the levator maxillae superioris and the levator palati from the side wall of the auditory capsule in front of the foramen facialis. The muscle is thick, and roughly cylindrical at its origin, but flattens out and becomes increasingly widened. Its posterior and superficial portions lie beneath the skin in the *anterior* wall of the spiracle. The direction of its fibres is generally ventrad, cephalad and laterad from their origin. The fibres which form the anterior wall of the spiracle are inserted into the distal end of the hyo-mandibular cartilage. The fibres arising most anteriorly are also the most median of the muscles; they swing almost directly cephalad and ventrad to be inserted into the exceedingly strong fibrous binding between the palato-quadrate and the mandible just lateral to the joint. The fibres between these two sets descend almost to the same ventral level, but, instead of gaining attachment to the fibrous investment of the cartilages between the other two insertions, turn mediad and caudad and join the cranio-glossus muscle.

The cranio-glossus (Cr.gl.).—This muscle takes origin from the side wall of the auditory capsule deep to the levator hyo-mandibularis; it passes down in the side wall of the mouth in front of the spiracle, forming the deeper portion of the anterior wall thereof. Arrived at the floor-level, the muscle turns mediad beneath the mucosa of the floor to the midline. The anterior fibres trend forward to be inserted into the posterior edge of the mandible not far from the symphysis. The posterior fibres are inserted into the anterior edge of the hypo-hyal and the lateral edge of the basi-hyal in front thereof. Between these two extremes the fibres are inserted into a median raphe. Those fibres which are inserted into the hypo- and basi-hyal pass ventral to the hyo-glossus to reach their insertion. The rest of the muscle is submucous, and dorsal to the visceral skeleton.

As viewed from the lateral aspect, the adductor hyoidei appears as a single entity with two insertions and a median portion whose fibres pass mediad out of sight without any insertion. As viewed from the medial aspect the pars cranio-glossus is distinctly definable from the rest of the muscle from about half-way down the descent from the origin. A little lower the two portions become completely separated.

The hyo-glossus (Fig. 16).—This we regard as the second oblique subarcual muscle, which has increased in size, lost its attachment to the postero-dorsal aspect of the basi-hyal and joined its fellow of the opposite side. The reduction, almost to extinction, of the cerato-hyal, as demonstrated by de Beer (1932), has been accompanied by the transfer of the origin of this muscle to the lower end of the hyo-mandibular.

Each half of the combined muscle is triangular, the broad end being at the midline where it meets its antimere ; from here it tapers to its origin, by a short strong tendon, from the antero-superior edge of the hyo-mandibular immediately behind the lateral insertion of the adductor hyoidei, that is, close to the lower end. The muscle is placed immediately beneath the mucosa and lies on the floor of the mouth between the two spiracles.

The relation of the spiracle to these muscles and to the hyo-mandibular cartilage now calls for attention (Figs. 15, 16).

The hyo-mandibular cartilage is articulated to the skull behind and below the auditory capsule. From this position it curves laterad, ventrad, and cephalad, round the posterior margin of the spiracle. Posteriorly it lies against, and is easily separated from, the anterior face of the first gill wall, which latter carries the pseudo-hyal cartilage, immediately behind the hyoid interbranchial muscle. The hyo-mandibular cartilage is covered dorsally for the first half of its length by the levator hyoidei, below that it is bedded against the propterygium and its muscles. Its anterior surface is covered for the greater part of its length by the skin of the posterior spiracular wall. Immediately in front of the origin of the levator hyoidei from the side wall of the cranium, and blending with it, is the origin of the adductor hyoidei ; this muscle curves round the anterior wall of the spiracle to gain its insertion into the distal end of the hyo-mandibular cartilage. The posterior spiracular wall gains thickness as it slopes caudad, the anterior has full depth, supplied by the two portions of the adductor hyoidei. Immediately within its outer boundary the lateral narrow end of the hyo-glossus muscle is found on the floor of the spiracle. The roof of the spiracle is supplied by the blended origins of the levator and adductor hyoid muscles, and by the side wall and base of the skull medial to them.

Raja.—The adductor hyoidei in this form is not divisible into two portions as in *Dasyatis*. Here we have only the portion which was described as the levator hyo-mandibularis. These fibres which in that form turn caudad to join the cranio-glossus are, in this, inserted into a fibrous band which connects the other two insertions. Marion described that portion of this muscle which bounds the spiracle the Csd.1 (p. 11), and the rest he regarded as a thin deep layer of the levator maxillae superioris. True, in *Raja* the insertion is carried round the lateral wall of the mouth and across the anterior, or superior, wall onto the maxilla for some distance. But in *R. australis* I find the muscle readily separable from the overlying levator maxillae superioris and, furthermore, the hyoid muscle is very definitely innervated from the hyo-mandibular branch of the facial, whilst the levator maxillae, a mandibular muscle, is just as definitely innervated from the mandibular division of the fifth nerve. There may be some overlapping of the nerves, but the obvious innervation is as stated.

The hyo-glossus.—This is the muscle which Marion designates (p. 33) the coraco-hyo-mandibularis. The muscle is relatively more extensive than in *Dasyatis* and extends further caudad, so that its lateral fibres have a direction caudad with an inclination mediad. The tendon of origin is longer.

It were quite misleading to adopt Marion's designation. de Beer has observed the muscle in *Torpedo* (1932, p. 312) and remarks that " it is not an ordinary coraco-hyoid muscle ". It is innervated from the hyo-mandibular division of the facial nerve, not by the spinal accessory. Its posterior limit is far short of the coracoid and none of its fibres are inserted into any fascia which is bound to the coracoid. It is entirely dorsal to the basal branchial elements.

THE HYOID DEPRESSOR.

Dasyatis.—The coraco-hyoideus is a stout, nearly cylindrical muscle which takes origin from the anterior edge of the first ventral extrabranchial cartilage and the deep surface of the coraco-arcuales fascia superficial to it. The direction of the fibres from origin to insertion is cephalad and dorsad. The insertion is onto the lateral edge of the hyoid copula.

Raja.—Marion's description of the muscle in *R. erinacea* correctly describes the condition in *R. australis*. Attention is drawn to the insertion onto the hypo-hyal cartilage in place of onto the basi-hyal.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Superficial Constrictors. (Figs. 15, 16.)

A. Dorsal.—There appears little doubt that in the selachians the more superficial portion of that muscle which, in its deeper portion, forms the levator maxillae superior, is the representative of the primitive dorsal constrictor sheet in the mandibular segment. In the batoid elasmobranchs there is developed as the anterior margin of the spiracle a muscle which, from its innervation entirely by a post-spiracular branch of the facial nerve, is identifiable as a pre-spiracular hyoid muscle, the adductor hyoidei. In front of this there is an elongated muscle which must undoubtedly be identified as the levator maxillae superioris.

Dasyatis.—The latter muscle arises from the anterior wall of the auditory capsule and the inner wall of the orbit behind the foramen quadringomini. It is a relatively long, strap-like muscle, and passes from its origin cephalad and ventrad and slightly mediad immediately beneath the oculo-motor muscles to an insertion on the superior margin of the upper jaw a little to one side of the symphysis.

The relation of the muscle to the maxillo-mandibular trunk of the fifth nerve calls for comment. The origin of the muscle is behind and lateral to the nerve foramen, and in its course to its insertion it passes beneath the nerve, lifting it away from the subjacent hyoid pre-spiracular muscle. The division of the nerve into maxillary and mandibular rami takes place on the dorsal surface of the muscle. The maxillary ramus is continued forward immediately beneath the floor of the orbit, the mandibular ramus passes ventrad across the muscle not far to one side of its insertion. The motor twig to this muscle is given off just after the separation of the two rami.

In *Raja* the muscle is essentially as in *Dasyatis*. It is that which Marion described as the dorsal part of the levator maxillae superioris.

B. Ventral.—In both *Dasyatis* and *Raja* the pars intermandibularis (Csv.1a) is a very thin and narrow band of fasciculi which, interrupted by a median tendinous raphe, extends between the two lower jaw rami. The pars extramandibularis (Csv.1b^2) is a stronger band of fasciculi. This also takes origin from the median ventral raphe and is inserted in *Dasyatis* by a fine tendon into the extreme lateral end of the mandible just lateral to the joint, but medial to the symplectic. In *Raja* the insertion is into the ventral edge of the mandible medial to the joint, and this insertion is as extensive as the muscle is broad.

The Deep Mandibular Constrictors.

It is believed that the levator is represented by a thin ribbon of muscle, the levator palatini (Fig. 15, L.pal.), which lies between the levator maxillae and the pre-spiracular hyoid muscle. This takes origin from the skull between the origins of those muscles and passes down beneath and in contact with, the levator maxillae to be inserted into the roof of the mouth behind the insertion of that muscle. It is innervated by the same twig of the mandibular ramus of the fifth nerve that innervates the levator maxillae superioris.

In *Raja* the muscle is not differentiated from the levator maxillae which must therefore be regarded as representing the constrictor and the levator.

The Mandibular Adductors. (Figs. 15, 16, 17.)

Although considerably modified by the separation of the maxillo-mandibular arcade from the skull, it is not difficult to recognize in the rays the same components of the adductor mass that were described in the selachians and in *Heterodontus*.

The Oblique Epiarcual Muscle.

In *Dasyatis* the oblique epiarcual, pterygoideus muscle (Pt.a., Fig. 15) is an elongated, flattened, relatively stout muscle which takes origin from the antero-ventral margin of the optic fenestra in the side wall of the cranium. This origin is by a very short tendon which invests the end of the muscle. From this origin the muscle passes cephalad and slightly laterad in contact with the floor of the sphenoidal cavity of the cranium. In front of this it is in contact with the under surface of the floor and posterior wall of the nasal capsule ; it next turns ventrad across the anterior surface of the upper jaw. Having passed the upper jaw it turns caudad and, after traversing the soft tissues in the side wall of the mouth lateral to the common insertion of the two labial muscles, ends in a relatively long and very strong tendon which burrows into the medial adductor mandibularis not far from its medial border and is inserted onto the postero-inferior edge of the *lower* jaw at about the junction of the outer and middle thirds of its length.

This muscle lies upon the levator maxillae (mx.s.) at its origin and is at that point medial thereto. As it passes forward and ventrad, it crosses the levator so that at the insertion of the latter it lies lateral to it. The division of the fifth nerve trunk into maxillary and mandibular rami takes place just after the nerve comes to lie against the lateral edge of this muscle dorsal to the levator. The mandibular division follows the lateral edge of the pterygoid muscle till its tendon disappears between the fasciculi of the quadrato-mandibularis. Motor branches to the pterygoideus, maxillo-labialis and partes posterior and medialis of the quadrato-mandibularis are given off before the tendon is crossed, those to the partes anterior and ventralis and to the mandibulo-labialis after it is crossed.

Taeniura (Fig. 17).—The pars anterior of the pterygoideus (Pty.a.) is almost precisely the same as in *Dasyatis*; in that form no pars medialis was recognizable. The pars posterior (Pty.p.) is a relatively small flattened muscle which arises from the palatoquadrate just in front of the lower end of the pars anterior and its tendon. It is inserted behind the tendon onto the outer surface of Meckel's cartilage.

Raja.—This muscle has been described by Marion (p. 22) as the first part of the levator labialis superioris, a most misleading designation, justified only by its homology with the similarly named muscle in the Selachii. It is relatively a smaller muscle than in *Dasyatis* and takes origin further forward, from the floor of the nasal capsule. Its insertion is, however, precisely similar, and the mandibular ramus of the fifth nerve lies to its outer side from origin to the dipping of the tendon just as in the other form.

THE MANDIBULAR ADDUCTOR, QUADRATO-MANDIBULARIS. (Figs. 15, 16, 17.)

Dasyatis.—(1) The pars medialis (Qm.m.) arises by a short investing tendon from the ethmoid region of the skull above the posterior wall of the nasal capsule and, swelling into a fairly stout flattened muscle, passes ventrad, cephalad and laterad. It penetrates between the massive partes anterior and posterior and, passing superficially to the dorsal edge of the pars anterior, is inserted onto the posterior edge of the lower jaw just below and lateral to the joint. (2) The pars posterior (Qm.p.) is particularly massive; it takes origin from a small area on the lateral surface of the palatoquadrate close to the joint. Increasing very rapidly in size, its lateral fibres curve round the pars medialis to be inserted almost alongside their origin, on the other side of the Q-M. joint, onto the posterior tip of the lower jaw cartilage; this tip lies behind and lateral to the joint. The symplectic cartilage is bound to Meckel's cartilage immediately behind and medial to its postero-lateral end and the fibrous strands of the capsule of this joint are continued across the lateral face of Meckel's cartilage to the capsule of the Q-M. joint. The band of fibres in question separates the insertion of the much-curved lateral fibres of the pars posterior from the insertion of the rest of the muscle, which is onto the posterior edge of Meckel's cartilage for a short distance medial to the band. (3) The pars anterior (Qm.a.) takes origin from a prominent tubercle on the outer surface of the palatoquadrate just in front of the joint, and from the surface of the cartilage between the tubercle and the attachment of the oral mucosa. The area extends from the posterior limit of the teeth to the capsule of the joint. The muscle increases in bulk as it crosses directly to be inserted onto the whole width of the outer surface of Meckel's cartilage for the posterior and lateral half of its length. The anterior limit of this portion of the muscle is very clearly determined by the tendon of the pterygoideus muscle. (4) The pars ventralis (Qm.v.) arises from the tissues in the side wall of the mouth in front of the pars anterior, from which it is separated by the tendon of the pterygoidal muscle, and is inserted in front of that tendon onto the outer surface of the lower jaw. This is quite a small muscle.

The terminal branch of the mandibular ramus of the fifth nerve, after giving off the motor twigs to the partes ventralis and anterior, passes along the anterior margin of the pars anterior, on its way to the ventrum of the jaw.

Comparison of these adductor muscles with those of *Acanthias* and *Heterodontus* discovers features of particular interest. The pars medialis arises from the skull as in *Acanthias*, but passes over the pars anterior to be inserted behind it as in *Acanthias*. The pars posterior is much more massive than in either of the other forms and its origin has extended over the insertion of the pars anterioris and reached the palatoquadrate superficially to it. The pars ventralis is much smaller than in the other forms. The origin of the pterygoideus muscle is peculiar.

but its relation to the mandibular nerve and its insertion leave little room for doubt that it has been correctly identified.

Taeniura (Fig. 17).—The pars medialis (Qm.m.), as is usual, arises from the post-orbital angle of the skull. This origin is by a short rounded tendon and the muscle swells rapidly into a short thick rounded body which penetrates between the partes anterior and posterior, being almost completely enswathed by the latter. The muscle contracts rapidly and is inserted onto a spur at the lateral, posterior, end of Meckel's cartilage. This spur projects dorsal to the palatoquadrate, between it and the hyo-mandibular and is post-articular.

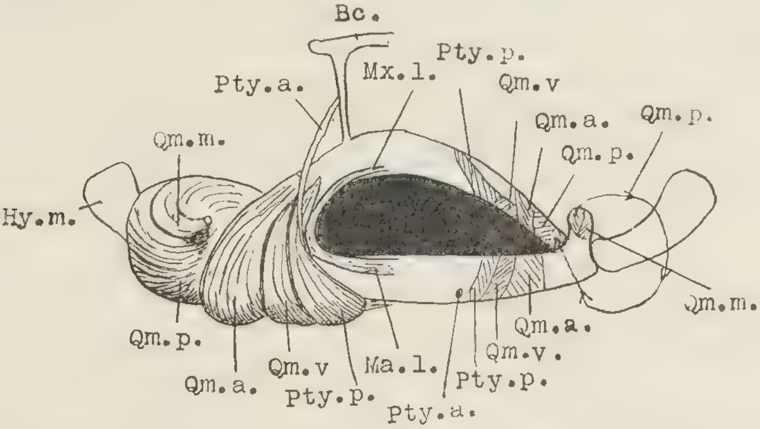


Fig. 17.—*Taeniura*. A slightly schematic drawing of the mandibular adductor muscles, seen from in front.

The pars posterior (Qm.p.) arises from the palatoquadrate just in front of the Q-M. joint, and swings right round the outer aspect of the pars medialis to be inserted onto the same spur of Meckel's cartilage.

The pars anterior (Qm.a.) arises from the palatoquadrate just in front of the origin of the pars posterior, and passes, with a curve ventrad and mediad, to be inserted onto the posterior end of Meckel's cartilage in front of the joint.

The pars ventralis (Qm.v.) arises from the palatoquadrate at the angle of the gape just behind the pars medialis of the pterygoideus muscle. The origin is confined to a very short length of the edge of the mandible, in line behind the teeth, and extends slightly onto the outer surface. The deeper fibres arise, not from the cartilage, but from the fibrous tissues of the side wall of the mouth behind the gape. The insertion is onto the inferior and posterior surface of Meckel's cartilage between the pars anterior of the quadrato-mandibularis and the pars medialis of the pterygoideus.

The relation of the mandibular ramus of the Vth nerve to these muscles is as in *Dasyatis*.

In *Raja* the muscles are essentially similar, but their interpretation by Marion is so different from that adopted above that it is advisable to review briefly the differences and to identify the parts of the muscle in *Dasyatis* with those of this standard batoid type.

Raja.—(1) The pars medialis is that muscle which Marion describes as the second division of the levator labialis superior. The muscle has the same origin as in *Dasyatis*, but loses its identity in the substance of the pars posterior. (2) The pars posterior is the superficial portion of the adductor mandibulae lateralis of Marion's description. The arrangement of the portion is essentially as described, but there is a very complete blending of this and the partes anterior and medialis. An added complication of the picture is caused by the fact that many of the fasciculi of all three parts take origin from, or are inserted into, a very strong superficial fascial sheath. (3) The pars anterior corresponds to the deep portion of the adductor mandibulae lateralis of Marion. There is here no noteworthy difference. (4) The pars ventralis is essentially the same in both forms; it was not described by Marion.

The relation of the mandibular ramus of the fifth nerve is essentially similar in the two forms.

This comparison of the muscles in the two forms permits one to believe that, though those of *Dasyatis* are very intimately blended, they present the same fundamental arrangement as was observed in the selachians and in *Heterodontus*, and that the conditions presented in *Dasyatis*, wherein the muscles are not so intimately blended, provide us with an analysis of the muscles in the Rays generally.

In addition to the muscles already described, there are in *Dasyatis* two labial muscles. These I designate maxillo- and mandibulo-labialis respectively. Each takes origin from the subdermal edge of the upper or lower jaw to one side of the symphysis and passes laterad across the outer surface of the cartilage in the tissues of the lips at the angle of the gape. They are inserted in the tissues of the angle of the gape so closely together that it was at first thought that one had found an orbicularis oris which arose from one jaw and passed around in the lips to be inserted in the other. They are small cylindrical muscles.

In *Raja australis* there is only the mandibulo-labialis; it was described by Marion as the adductor mandibularis medialis. His statement that in his species of *Raja* the origin of the muscle was from the anterior edge of the upper jaw suggests that both muscles are really present, but that he failed to discover the duality.

Doubtless these are specialized portions of the adductor complex, but I have been unable to find any muscles in any of the other elasmobranchs which are comparable with them.

The Trapezius.

Dasyatis.—For some distance posterior to the skull the spinal segments are completely fused. The dorsal capiti-nuchal muscles are inserted by a cord-like very strong tendon into the dorso-posterior edge of the skull on each side of the foramen magnum. The branchial atrium extends a good distance posterior to this point. The capiti-nuchal muscles enlarge steadily as they pass backwards and are packed close against the crest formed by the fused dorsal spinal processes and enclosed in a very strong fibrous trough. At a distance behind the skull which is almost equal to the length of the cranial and sphenoidal cavities the scapula is attached to the fused lateral spinal processes. These latter, in front of this attachment, send a vertical flange dorsally, forming an outer wall to the trough of the capiti-nuchal muscles. The scapula is relatively very broad antero-posteriorly and extends forward of its attachment to the spinal column. There is thus formed a triangular space whose medial wall is the vertical flange formed from the fused lateral spinal processes; this slopes from behind forward and mediad. The outer wall, the scapula, slopes from behind forward and laterad. The anterior wall is the convex posterior wall of the branchial antrum. The roof of this space is the deep superficial dorsal fascia; its floor is in part the lateral portion of the roof of the pericardium, and lateral to that the dorsal surface of the pars posterior of the coraco-branchialis muscle.

This space is filled by the trapezius muscle, which takes origin from the inner wall and is inserted onto the outer.

Raja.—The muscle is essentially as above, but there is no cartilaginous outer wall to the sheath of the capiti-nuchal muscles. I can find no trace of the three divisions of the muscle described by Marion. The trapezius is innervated by spinal muscles.

The Ventral Longitudinal Hypobranchial Spinal Muscles.

These are, of course, the depressors of the mandibles, but, as they are not developed from cephalic myotomes, they have not been included in the table.

They are so essentially similar in both forms and follow so closely the conditions described by Marion that it were mere repetition to describe them.

The close similarity of the coraco-hyoideus to the separate portions of the coraco-branchialis justifies one in feeling doubtful as to whether the coraco-hyoideus of the Elasmobranchii is the same muscle as that of the bony fishes. In these latter there appears to be complete agreement that the muscle is developed from trunk myotomes, and it has a very definitely antero-posterior direction. On the other hand, there is not such complete agreement as to the derivation of the coraco-hyoideus of the Elasmobranchs. van Wijhe (1882) describes the muscle as being developed equally from the posterior head myotomes and anterior trunk myotomes, whilst Neal (97) and Edgeworth (1911) are in agreement in deriving the muscle entirely from trunk myotomes. In addition to the doubt this difference of interpretation gives grounds for, the muscle in the cartilaginous fishes commonly appears as though it were a separated portion of the coraco-branchialis.

4. Review.*

An appeal to embryology does not give the student of serial muscular homologies assistance of that definite kind which might have been expected. It has been demonstrated that the whole of the muscles related to any one branchial arch are developed from a single branchial muscle plate, that the muscles developed from the hyoid muscle plate are innervated by the facial nerve, and that those innervated by the fifth nerve are developed from the mandibular plate.

There are exceptions to the complete truth of the above statement, but the exceptions are for the most part taken cognizance of in the designations epibranchial and hypobranchial "spinal" muscles. The apices of the mandibular and hyoid muscle plates are broken off and divorced from the rest of the plate to give rise to two of the ocular muscles; they will be discussed later, in Appendix A.

The evidence of the embryologist, however, is not against, but rather supports, our fundamental concepts of the course of the evolution of the segmentally arranged visceral muscles. The embryologist, except in isolated cases, is unable to offer any evidence of those more primitive conditions which it is believed the hyoid and mandibular musculature has passed through prior to the perfection of the profoundly modified muscular and skeletal mechanism which we find in these anterior two segments of even the most primitive of the forms available now for study.

Studies of the skeletal and muscular structure of the vertebrate head appear to justify the following beliefs:

The primitive vertebrate from which the whole of the recent forms and their fossil allies were evolved was possessed of a terminal or subterminal mouth, and had behind it seven gill slits on each side of the head. The mouth led into a respiratory antrum, into which the gill slits opened. Each of the slits carried branchiae on both walls. These walls were provided with unjointed cartilaginous supports, and each was also provided with a simple sheet of muscle fibres which was capable of acting as a constrictor and which was antagonized by the elasticity of the cartilaginous support. It was from those simple hoops that the branchial skeleton, as we now see it, was evolved. But further than that, it appears probable that all the seven hoops were modified in the same way originally. The mandibular and hyoid skeletons were precisely similar to the others. Their muscular equipment became modified and adapted to the later changes in the framework. Weak points were symmetrically developed in the hoops, at their centres and above and below those centres on each side; these were replaced by joints and there resulted pharyngo-, epi-, cerato- and hypo-branchial segments on each side. Whether a ventral continuity of the hoops of the two sides was original or whether a basal element was added is immaterial to the present discussion. The deeper portion of the constrictor sheet of muscle fibres would have been bound to the cartilaginous hoop. When that hoop became segmented, the attached fibres were similarly segmented, and their binding to the hoop in the immediate vicinity of the joint was relaxed whilst their attachments immediately above and below became more perfect.

Thus, it would seem, the primitive muscle sheet became differentiated into a more superficial, almost unchanged, constrictor portion and a deeper portion divided into dorsal, middle and ventral flexors of the three joints of the arches.

With the disturbing growth of the brain there resulted marked changes. The resulting flexure of the head ventrad appears to have been accompanied by, and perhaps to have been responsible for, the coalescence of the anterior gill slit and the mouth. The primitive mouth was at once replaced by this newer one. All that now remains of the original oral musculature are the four primitive ocular muscles. The apices of the hyoid and mandibular muscle plates became captured by the (new) preoral segment to supply the two extra ocular muscles (*vide* Appendix A). Extra respiratory surface was obtained in the gill clefts without increasing the bulk of the branchial region by the oblique caudad growth of their walls so that they came to overlap.

More important changes, however, were those of the mandibular arch and its related muscles. There is evidence in almost every one of the fishes, that the dorsal and ventral ends respectively of all the epibranchial and ceratobranchial cartilages could be brought into close approximation

---

* This review is confined to an examination of the serial homology of the muscles related to the seven visceral arches of the previously reviewed Elasmobranchii. Their homology with muscles in other vertebrates will be discussed after those other forms have been described.

by the action of the constrictor sheet and the two or three flexor muscles of the arches. In the case of the mandibular segment not only was this so, but when the gill slits and mouth coalesced or were opened into by the backward extension of the primitive mouth (de Beer, 1931), the ventral ends of the ceratobranchials of the two sides became joined in the symphysis of the lower jaw, whilst the dorsal ends of the two epibranchial cartilages were welded together in similar manner to form the symphysis of the upper jaw. The elements of this first arch above and below these were reduced, but perhaps persisted as the labial cartilages. The labial cartilages, may, however, be persistent branchial rays.

The opposed anterior ends of the mandibular cartilages now were brought into use as upper and lower jaw, and were increased in size and modified in other ways to carry out those functions more efficiently.

These cartilages and their activating muscles were increased very much in size, growing forward as the unfolding of the ventral cephalic flexure permitted, or indeed, perhaps, actually conditioning that unfolding. With their increase in bulk, these cartilages came nearer to the surface and, as it were, grew forward through the superficial constrictor sheet, which was attached above and below to superficial structures which were not carried forward with or by the forward growth of the mandibular skeleton. The deeper, specialized, muscles attached to the arch were, on the other hand, carried forward attached to the dorsal and ventral ends of the two middle elements and to the vanishing elements of the arch above and below them. Muscles evolved from these rests are recognizable, but profoundly modified.

Perhaps another result of the ventral flexure of the head was that there developed a biotactic stimulus between the anterior point of the ventral trunk myotomes and the ventral ends of the branchial arches. Whether this be the explanation or not, the anterior end of the trunk myotome grew forward, displaced to either side the ventral ends of the branchial constrictors, and, burrowing deep to the hyoid and mandibular ventral constrictor sheets, gained an attachment to the ventral, mandibular arcade.

This anterior hypobranchial spinal musculature immediately functioned as a depressor of the lower jaw, and later also assumed the functions of a general branchial depressor. To this end the branchial muscle plates also developed special slips of muscle (the coraco-branchialis) which acquired insertions either into the aponeurosis of the hypobranchial muscles or onto the ventral portion of the pectoral arch. It is also not improbable that the crowding effect of these hypobranchial muscles is reflected in the reduction of the cerato- and hypo-branchial elements, so commonly seen in the Elasmobranchs.

With the assumption of oral and prehensile functions the mandibular arch had need of firmer fixation of the middle joint. The remarkable growth of the two cartilages may be supposed to have already largely suppressed the gill cleft immediately behind it. This permitted the second arch to be brought into use to provide the needed fixed point, and hyostylic suspension resulted.

It is clear, on the evidence of the facts as we now see them, that the ventral elements of the hyoid arch grew forward between the increasing cerato-oral cartilages. Now, there was, ex hypothesi, no direct muscular and fibrous union between these two arches ventrally and the second had to be prevented from sagging below the first. This was effected by the retention and strengthening of the first two constrictor sheets ventrally.

The second arch had now also completely lost its respiratory function, its dorsal portion acting as a suspensorium of the first and its ventral elements, placed in the floor of the mouth, were called upon to function as assistants in the passage of food back towards the oesophagus, their musculature being modified accordingly. Not only was this so, but the closure of the gill slit, except for the small persistent spiracle dorsally, gave rise to an immobile area between the mouth in front and the respiratory antrum behind. This must not be left flaccid, and the need was met by increase in the bulk and strength of the dorsal and lateral portions of the second constrictor sheet and the levator.

Finally, it appears not too much to believe that we have here the explanation of that persistence of the second constrictor sheet, which we find throughout the whole vertebrate series.

The foregoing working hypothesis is based very largely on the development and adult anatomy of the branchial arches. Throughout the Plagiostomi there are certain constant features which must surely be regarded as inherited direct and almost unchanged from a common ancestor.

The skeletal framework is constantly composed of four segments joined to a median basal element. The muscles of each interbranchial septum are :

1, An entirely superficial constrictor sheet which, following Lightoller, we have designated the pars arcuata. This lies between two clefts immediately beneath the skin.

2, A constrictor sheet quite continuous with the last, placed in front of it ; quite superficially above the level of the gill clefts, but passing under the pars arcuata of the septum in front of it and onto its own septum anterior to the gill rays thereof, and supplying that portion of the septum which lies between the edge of the cleft and the outermost ends of the branchial rugae. Ventral to the gill cleft it becomes superficial, again continuous with and in front of the lower portion of the pars arcuata. We have termed this the pars inscriptionalis, again accepting Lightoller's designation.

3, A third constrictor sheet which is related to the second precisely as the second is to the first. This we have termed the deep dorsal constrictor or interbranchial muscle. It does not become superficial in any part. Its position is antero-medial and deep to the second sheet, lying anterior to the gill rays and posterior to the branchial rugae. These three portions are absolutely constant in every interbranchial septum throughout these cartilaginous fishes and together they constitute an unchanged " rest " of the primitive constrictor sheet. Of the three parts the deep constrictor is the most primitive. Partes arcuata and inscriptionalis are later, caudad, growths. Even part of the deep constrictor is an added structure, for the primitive gill slits were shallow and led directly, without any obliquity, from the atrio-pharynx.

Though, in conformity with past practice, these three have been treated as separate muscles they undoubtedly constitute one continuous interbranchial sheet. It will avoid ambiguity and assist brevity in later discussion if we designate the sheet the *pars primitiva* of the branchial musculature.

4, A levator arcus branchialis. This, like the partes arcuata and inscriptionalis, takes its origin from the fascia dorsalis and/or from an extrabranchial cartilage which is bound to that fascia, and it is inserted onto the epibranchial cartilage. We know nothing of the development of this muscle in the Elasmobranchs. Unfortunately it is but poorly developed or differentiated in the forms whose development has been studied. On the other hand, the muscle is not always completely differentiated from the dorsal end of the deep dorsal constrictor, and we are able to say with a high degree of confidence that it is a specially modified portion of that muscle. Our evidence in this respect comes largely from the conditions described in *Heterodontus*.

5, A small muscle which lies in the angle between and behind the pharyngo- and epibranchial cartilages ; this has been designated one of the " lateral series of dorsal interarcual muscles " ; in the foregoing pages it has been described as the dorsal oblique (epiarcualis obliquis) and classified functionally as the dorsal branchial adductor muscle.

6, An adductor arcus branchialis, which has been classified as the middle branchial adductor in the previous pages. This lies in the angle in front of the joint between the cerato- and epibranchial cartilages. These two adductors are developed from the deep part of the primitive branchial muscle plate.

7, A depressor arcus branchialis. The several depressors are combined to form the coracobranchialis muscle ; they are developed from the lower ends of the branchial muscle plates.

8, Incomplete subarcualia transversi are developed below the arches of certain Elasmobranchs. These are formed from the ventral ends of the partes inscriptionalis, which extend medially to gain insertions below the basibranchial elements.

9, In the great majority of the Elasmobranchs there are developed from trunk myotomes a series of muscles very similar to the dorsal branchial adductors but lying medial to them and extending always between segments of two arches. They have been designated epibranchial spinal muscles in the foregoing descriptions.

These are in many respects very similar to those ventral muscles which are present below the branchial skeleton of certain of the bony fishes, and there aptly designated subarcualia recti by Edgeworth. These latter, however, are derivatives of the branchial muscle plates and serve as a warning that muscles which seem similar may have completely different origins. This comment also applies to their similarity to the dorsal adductor muscles, with which they have, in the past, been classified. Marion designated these last the median series of dorsal interarcual muscles, following previous observers in so doing.

In closing this summary of the branchial musculature it may be finally stressed (1) that the components of the pars primitiva are absolutely continuous, each being placed in front of the other without interruption and the parts in front being each deeper than that behind, and (2) that the specialized muscles are developed from the deep part of the primitive branchial muscle plate.

In the hyoid segment there is nothing like the constancy of anatomical features which we find in the branchial segments. The variation in structure affects most strikingly the derivatives of the deep layer of the primitive plate. This we are able to state with a very high degree of confidence, because we find the pars primitiva almost unchanged and quite complete in all the typical Elasmobranchs, that is to say in the three suborders of the Plagiostomi. In the Holocephali and in the Chondrostei the first important modifications of this sheet are to be found, and the parts are not at once so clearly recognizable.

In the Plagiostomi, the pars primitiva is found in the typical situation relative to the gill cleft behind it. The pars arcuata is quite superficial and takes its origin above from the fascia dorsalis, exactly as does that part in the branchial segments. In front of it the pars inscriptionalis above the level of the gill slits has its origin just precisely as in the segments behind. There is here, however, no gill pouch in front for it to pass behind, and it is superficial throughout its length. The pars arcuata lies in the free edge of the gill slit and the pars inscriptionalis lies in contact with the outer ends of the hyoid gill rays. In front of this again is a similar sheet of fibres in contact with the inner ends of those rays, just as the deep constrictor lies against the inner ends of the branchial rays. Compare this with the interbranchial septum from another angle: If one examine the posterior face of a typical interbranchial septum one observes the mucosa covering the cartilaginous arch at its deep margin; next to this one finds the branchial rugae, and outside these the smooth lining of the free edge in which lies the pars arcuata. Radiating laterad and caudad from the epi- and cerato-branchial cartilages are the gill rays. On the side of these, faced anteriorly and laterally, we find the deep constrictor close to the main cartilages, and the pars inscriptionalis between this and the pars arcuata. Covering these anteriorly are the branchial rugae deep within the pouch and the skin more superficially over the pars arcuata. In the anterior wall of the first pouch there is an arrangement of structures which differs only in that there is no gill anterior to the muscular layer; this layer is the pars primitiva of the hyoid segment. It is not so much that the closure of the hyoid gill cleft has permitted the pars primitiva to reach the surface as that there has been no posterior growth of the pars primitiva of the segment in front to submerge it. There is no evidence of any backward growth of the primitive mandibular muscle plate in the development of the muscles of the mandibular segment. This we might have anticipated from a consideration of the adult anatomy.

Since we are able thus to recognize with confidence the pars primitiva of the hyoid segment and find it essentially as in the branchial segments, we may infer that the specialized muscles also were probably developed, but have now become modified in adaptation to the changed mechanical and skeletal conditions.

We have very clear evidence that superficial parts of the pars primitiva have been added behind the deeper muscles in this as in the branchial segments. We, therefore, look for the modified derivatives of those deeper muscles in front of the primitive sheet and probably deep to it—probably deep, but not necessarily so. It is obvious that, if, as it is believed, the mandibular arcades were deeply placed, they have now become actually subdermal in places. They have also apparently carried the attached hyo-mandibular cartilage towards the surface with them. Therefore, if we find muscles innervated by the facial nerve placed superficially in front of the pars primitiva of the hyoid segment, we are entitled to conclude that they are derivatives of the deep specialized muscles of that segment, carried to the surface in harmony with the changed skeletal structures to which they are or were attached. Further than this, the profound modification of the skeletal arch, its firm articulation, on the one hand with the skull and on the other with the mandibular arcades, and the disproportionate growth of some of its parts and more or less complete disappearance of others should prepare us to find the points of origin and insertion of those muscles quite different from their primitive positions.

In the branchial arches we find the levator to be dorsal and lateral to the dorsal adductor muscle, so that, were the pharyngobranchial cartilage lost and the epibranchial became articulated to the skull, whilst both these muscles were retained and were to retain their insertion onto the epibranchial cartilage, we should find the levator lateral, and that means superficial, to the other. Now, the skeletal changes just postulated are those which are believed to have taken place in the hyoid segment. In the Batoidei we find two muscles arising from the fascia dorsalis and the skull and inserted onto the epihyoid (hyo-mandibular); the more superficial may be regarded as derived from the levator and the deeper as from the dorsal adductor.

In addition to these there is also in *Heterodontus* a muscle which arises from the hyomandibular and is inserted into the posterior edge of the palatoquadrate and which is undoubtedly a hyoid muscle because it is innervated entirely by the hyo-mandibular branch of the facial nerve. This insertion of a muscle developed from the muscle plate of one segment onto a skeletal element of the segment in front is a secondary feature. It is not uncommon for ventral muscles to grow forward and/or backward to other than their segments of origin in the Teleosts. In the present case, however, the conditions are not exactly comparable, for the attachment of this hyoid muscle to a mandibular element has involved no growth anterior to its, presumed, primitive attachment. The muscle in question may be regarded as a derivative of the middle adductor of the hyoid arch. The joint of the hyo-mandibular cartilage with the posterior end of the mandibular arcade is placed close to the ventral end of the former, and therefore intervenes between the origin of the middle adductor and its primitive insertion onto the ceratohyoid. This then is to be regarded as the explanation of the insertion of the middle adductor onto the back of the palatoquadrate above the joint with the hyo-mandibular. The muscle we are describing is that which has been designated retractor mandibulae by previous observers. The origin of this muscle may be the primitive one from the hyo-mandibular, or, it appears, it may as a result of fusion with the dorsal adductor, gain an origin from the skull. In *Heterodontus* we find the more primitive condition; the muscle arises from the hyo-mandibular and is inserted onto the palatoquadrate cartilage. In the batoids the levator hyo-mandibulae and the cranioglossus appear to present more or less incompletely fused derivatives of the dorsal and middle adductor mucles, and these arise from the skull and are inserted onto the hyo-mandibular near its distal end and onto the palatoquadrate as well.

Although so similar to the component parts of the coracobranchialis, the coracohyoideus is one of the hypobranchial spinal muscles, and there is no true hyoid depressor.

Still limiting our observations to the Selachii we turn next to a review of the muscles of the mandibular segment.

In the consideration of the dorsal portion of the pars primitiva of this segment, there is one fundamental feature of adult anatomy and development which is apparently of prime importance. The spiracular cleft at no time presents any caudad superficial growth of its anterior wall. In the adult it differs from the other clefts in that its direction is almost at right angles to the long axis of the body. There has, then, been none of that backward growth which gave rise to the partes inscriptionalis and arcuata in the branchial segments.

It follows that we should find, of the pars primitiva, only the interbranchial muscle or deep constrictor. This is present but, because it lies against the outer edge of the spiracular cleft, in some forms appearing as a definite small hood, it has been designated by other writers the Csd.1 or the mandibular superficial dorsal constrictor. That which is conveyed by the separate tabular classifications of the muscles in each suborder, is now unequivocally stated, viz., this muscle is to be regarded as derived from the primitive constrictor sheet and believed to be actually serially homologous with the interbranchial muscles or deep constrictors of the hyoid and branchial segments.

The levator, so closely related to, and probably derived from, the deep constrictor, is commonly found in the mandibular segment to be intimately fused with, and in many cases inseparable from, the pars primitiva.

Of muscles derived from the specialized adductors there are, in the mandibular segment, apparently several. In the different plagiostome forms one finds muscles which at first sight are not comparable one with another. The study of many forms, however, leads to a better comprehension of those various muscles and it is realized that they are but modifications of one plan.

There is reason to believe that the quadrato-mandibularis or the adductor mass—composed as it is of relatively short fibres which pass without intermediate fibrous interruption from one ramus of the jaw to the other, from the cerato- to the hypo-arcual element—alone represents the primitive middle adductor of the mandibular arch. The complicated muscles anterior and superficial to this are to be regarded as having been derived from the dorsal adductor of the arch.

Unfortunately the evidence of embryology is not very helpful in the interpretation of the mandibular muscles. Edgeworth (1911, p. 179) says that in *Scyllium*, "On the formation of the palatoquadrate . . . the mandibular myotome lies outside of and across the palatine process, and then separates into an upper levator maxillae superioris and a lower adductor mandibulae ". Of the branchial muscles he says (p. 235) " Below the anlagen of the trapezius each branchial myotome forms a transversely broad plate in the branchial septum. The part internal to the branchial bar forms the adductor; the part external to the bar forms next the bar dorsally the arcualis dorsalis (our dorsal adductor), and below that the interbranchial, whilst the external edge forms the constrictor superficialis ". Here, in the branchial segments, the middle adductor is formed from that portion of the myotome which would lie ventral to the ceratobranchial cartilage if that cartilage were, like the cerato-oral (palatoquadrate), horizontal instead of vertical, whilst the dorsal adductor is developed from a portion which would lie above the bar. Edgeworth further states that the " upper edge of the adductor mandibulae (subsequently) gains an additional origin from the suborbital cartilage, and this anterior portion of the adductor separates . . . forming the levator labii superioris . . . " This origin of the anterior component of the adductor in *Scyllium* from the adductor anlage would appear to be in direct contradiction to my statement above that there is reason to believe that part only of the adductor mass is to be regarded as representing the primitive middle adductor of the mandibular segment.

On the other hand, it may be emphasized that the adductor alone is developed from that part of the branchial myotome which lies medial to the branchial arch, and that all the other muscles of the arch are developed from the rest of the myotome, whilst in the mandibular segment the ventral superficial constrictor also is developed from the portion which lies below the palatoquadrate. This portion below that bar is, therefore, not entirely homologous with that medial to the branchial bars. It contains the undifferentiated anlagen of more than one muscle.

The outstanding feature of the adult anatomy of the mandibular segment which would seem to indicate that the quadrato-mandibularis of the adductor muscle mass alone corresponds to the primitive middle adductor is the relation of the mandibular division of the fifth nerve to the muscles.

It becomes necessary here to refer to the mandibular adductors, not only of the Holocephali and Chondrostei, but also of the Teleosts and the Amphibians, including the Dipnoans. In all these one finds that there is a portion of the adductor musculature which takes its origin from the quadrate and is inserted onto the mandible. Both origin and insertion are close to the Q-M. joint and the muscle is separated from the rest of the adductor components by the mandibular and maxillary rami of nerve V. This is most strikingly seen in the Holocephali (Fig. 21) but is just as obvious in *Neoceratodus*. In *Psephurus* the two portions of the muscle are even more completely separated by the nerves. The separation of the pterygoid and other divisions of the adductor mandibularis by the same nerves is quite clearly seen in *Ichthyophis glutinosus* and in *Amblystoma tigrinum* and its immature Axolotl stage. In the adult Anura the relations, though somewhat obscured, are preserved unchanged, and are quite clear in the tadpoles.

These relations can also be demonstrated in the Teleostei.

It is neither necessary nor desirable to anticipate later sections of our work by entering on detailed descriptions of the features mentioned as being present in forms not yet reviewed. It is sufficient, having mentioned them, to draw the inference that a feature which is found constant in so large a range of vertebrate animals may be reasonably regarded as reflecting and resulting from a condition present in their common ancestor.

In short it must be regarded as an inherited character.

There is little doubt, then, that the portion of the adductor musculature which is found between the ramus mandibularis V and the joint is completely homologous in all the forms in which it is found, and it appears equally reasonable to assume that it is the persistent reappearance of the middle adductor of the primitive branchial musculature.

5. The Chondrostei.

PSEPHURUS.

In *Psephurus* there is observed a further stage in the reduction of the muscles in the branchial segments; the first stage is presented in the Holocephali.

I have had for dissection two very well preserved specimens which had a length over all of 30 cm. They were stained before dissection. I have also been able to dissect specimens of *Acipenser*, but as several species of that genus have already been fully described it is unnecessary to repeat the work (vide Vetter, 1878). The myology of *Polyodon* was described by Danforth (1913). His drawings so nearly represent the muscles of *Psephurus* that I have not thought it necessary to illustrate this description.

The innervation of the muscles in the acipenserids has been described by Norris (1925) and his work has saved me the necessity of tracing the motor nerves in my specimens.

PSEPHURUS.

		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial Constrictors	Dorsal ..	Absent	Levator operculi	Absent
	Ventral ..	Absent	Csv.2	Csv.1
Deep Constrictors	Dorsal ..	Absent	Lev., hy.	Protr.hy. (?)
	Ventral ..	Trans.v.vent.	Interhyoideus	Absent
Levators		Lev.arc.br.	Levator hyomandibulae	Protr.hy.
Epibranchial Spinal Muscles		Absent	Absent	Absent
Adductors	Dorsal ..	Absent	Absent	Pterygoideus
	Middle ..	Add.arc.br.	M.hyo-mandibularis	Quadrato-mandibularis
	Ventral ..	Sub.arc.obl.	Absent	Absent
Depressors .. .. Hyobranchial spinal muscles		Co.br.	Absent	Absent

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The superficial constrictors are quite unrepresented.

Of the deep constrictors, a single delicate subarcualis transversus, which extends between the basibranchial cartilages of the third arch, is the only representative found in my specimens.

Three levatores arcuum branchialium are present. They arise close together, one behind the other, under cover of the dorsal superficial hyoid constrictor, from the side of the cranium. They are relatively slender muscles and pass caudad, laterad, and slightly ventrad, to their insertions. The first is inserted into the upper ends of the first and second epibranchial cartilages, which are bound together by the tissue into which the muscle is inserted. The second is inserted in similar manner into the second and third, and the third into the third and fourth epibranchial cartilages. It follows that the first is the shortest and the third the longest of these.

Typical small adductores arcuum branchialium, middle adductors, are present in each of the arches except the last.

Three subarcuales obliqui are present. The first of these takes origin from the basihyal and runs out along the ventral surface of the first basi- and cerato-branchial cartilages to be inserted on the latter close to its dorsal end. The other two, much smaller, arise from the basi- and are inserted onto the cerato-branchial cartilages of the second and third arches.

The coracobranchialis muscle is represented by three bands of muscle fasciculi which take origin from the clavicle and pass dorsad, laterad, and cephalad, to be inserted into the median ventral edge of the fifth cerato-branchial cartilage near its ventral end.

The hypobranchial spinal musculature is represented by the coracohyoideus muscle. This is an unpaired cylindrical muscle which arises from the deep surface of the clavicle and from a superficial tendinous interruption to the other side of which the rectus abdominis is attached. The muscle tapers as it extends forward to terminate in a cord-like tendon which divides anteriorly. Each half is inserted onto the posterior and median edge of the inner end of the basihyoid of its side. Two other very fine but remarkably strong branches of this tendon on each side are attached to the inner ends of the second and third basi-branchial cartilages.

THE MUSCLES OF THE HYOID SEGMENT.

The condition of the constrictor muscles in *Psephurus*, as in other acipenserid forms, is of particular interest. These peculiar transition forms between the typical elasmobranch and teleost musculature provide the key to the understanding of the latter.

The superficial and deep dorsal constrictors appear as one continuous muscle, which from its insertion may be treated in two parts. (*a*) The levator hyo-mandibulae takes origin from the cranium under the lateral edge of the parietal bone. There is a vacuity in the dorsal cranial covering bones between the parietal and the suturing ends of the post-temporal and the dermosphenotic. The line of origin of the levator hyo-mandibulae commences in front about one-third of the length of the vacuity from its anterior end and occupies about the middle third of that length. From this origin the muscle passes ventrad, caudad, and slightly laterad, to be inserted onto the dorsal edge of the lateral surface of the hyo-mandibular, which is here subdermal. (*b*) The levator operculi arises in the same line behind the levator hyo-mandibulae and passes parallel to it to be inserted into the dorsal margin of the operculum. The two portions are quite continuous and are only described separately because of their separate insertions, and because previous observers have divided the muscle in *Acipenser* and in *Polyodon*. The sheet of muscle fibres is subdermal throughout their length; the dorsal cranial covering bones are but extensive dermal scutes. In their passage from origin to insertion they pass deep to the conjoined post-temporal and dermosphenotic. The muscle is innervated by twigs of the hyoid branch of the facial which passes deep to the hyo-mandibulo-cranial joint and winds superficiad, round the top of the hyo-mandibular cartilage. The twigs then course backward over the surface of the muscle.

The superficial ventral constrictors present the typical elasmobranch division into Csv.2 and interhyoideus.

The interhyoideus takes origin from the median ventral raphe behind, and partly under cover of, the Csv.1. The fibres pass laterad and slightly caudad to be inserted into the middle one-third of the length of the ceratohyoid along the median edge.

The Csv.2 is continuous with the posterior margin of the interhyoideus and it arises from the median ventral raphe behind it. From this origin the fibres pass laterad and caudad and then dorsad, behind the ceratohyoid, pseudohyoid* joint, along the free area of the opercular fold, to be inserted into the ventral edge of the splint-like suboperculum.

The muscle is innervated by twigs from the hyoid branch of the facial. This nerve, after becoming subdermal at the upper end of the hyo-mandibular, passes ventrad and caudad behind that cartilage under cover of the operculum, and then turns forward mediad to the ceratohyoid, crosses that cartilage superficially from behind and medially cephalad and laterad under cover of the suboperculum, and runs forward medially to the lower jaw. The motor twigs to the Csv.2 and interhyoideus are given off just before it crosses the ceratohyoid.

The middle adductor muscle of the hyoid arch is apparently represented by a small triangular sheet of fibres, the M. hyo-mandibularis, which arise from the deep edge of the anterior surface of the pseudohyal and are inserted into the posterior edge of the mandibular cartilage below the maxillo-mandibular joint. This little muscle may act as a depressor mandibulae or as protractor hyoidei.

The motor nerve for this muscle comes from the hyoid branch of the facial after it has crossed the ceratohyoid.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The intermandibularis (Csv.1) presents two portions. These, however, are not strictly comparable with the pars intermandibularis and pars extramandibularis of the typical Elasmobranch. Rather they foreshadow the pars submentalis and posterior of the Teleosts. A similar division of the Csv.1a has been described in *Mustelus* by Lightoller and in Acanthids by Marion. The pars submentalis is composed of short fibres which cross from one mandibular ramus to the other immediately behind the symphysis without any median interruption. The pars intermandibularis (Csv.1b) is a broader sheet of fibres which take origin from the mandibular ramus behind the first part and nearly as far back as the ramus extends. The fibres do not cross the mid-line but are inserted into a median ventral raphe. The posterior fibres incline caudad from the mid-line and overlap the insertion, but not the origin, of the interhyoideus muscle.

---

* The hyoid arch of *Psephurus* possesses a remarkably large interhyal cartilage. This, in the light of de Beer's (1932) work on the development of the hyoid arch in the rays and Sharks, I have designated the pseudohyoid, though I have not been able to check the identification by determining the position of the artery.

The levator maxillae superioris and deep dorsal constrictor of the mandibular segment in the typical Elasmobranchs are here represented by the remarkably developed protractor hyo-mandibulae. This muscle arises from the walls of a large sulcus in the side of the cranium. The sulcus extends forward above the orbit for some distance and backward behind the orbit to the cranio-hyo-mandibular joint. This is a massive spindle-shaped muscle whose thickest part lies between the orbit and the hyo-mandibular joint. The direction of the long axis of the muscle is from in front caudad, with an inclination ventrad and laterad. The muscle is inserted into the capsule of the hyo-mandibulo-symplectic joint.

The innervation is from the trunk of the fifth nerve immediately after it emerges from the trigeminal foramen. The innervation is somewhat peculiar in that the twig enters the deep ventral surface of the muscle immediately behind the orbit. It is unusual for the motor nerve to the muscles of the fishes to penetrate the muscle before breaking up.

The dorsal oblique adductor and the middle adductor muscles of the mandibular arch are both present.

The dorsal oblique (pterygoideus muscle) is the larger of the two parts of the adductor mandibularis of previous observers. It arises from the outer surface of the palatoquadrate cartilage right forward to the symphysis. Commencing as a quite thin muscle at the mid-line anteriorly, it increases in bulk as it extends back along the hollow of the expanding cartilage. Near the posterior end of the cartilage it turns sharply ventrad, passes through a check ligament and is inserted onto the outer and upper surface of Meckel's cartilage a short distance in front of the joint. The check ligament is a very strong band which arises behind from the fibrous capsule of the Q-M. joint, passes forward subcutaneously and then turns mediad beneath the buccal mucosa at the angle of the mouth and is inserted onto the deep surface of the same capsule.

The middle adductor (quadrato-mandibularis) is much the smaller component of the adductor musculature of the jaws. It takes origin from the outer surface of the expanded posterior and of the palatoquadrate cartilage. It tapers very rapidly and passes beneath the check ligament to be inserted onto Meckel's cartilage behind the pterygoideus and just in front of the joint.

These two muscles are not fused in any part. They are separated at their contiguous margins by a deep fissure in which is lodged the mandibular ramus of the fifth nerve. Both muscles are innervated by twigs from the mandibular V.

Psephurus, in its visceral musculature, is very similar, not only to the allied *Polyodon*, but also to *Acipenser*. I have tabulated below the muscles found in the latter by Vetter (1878) and in the former by Danforth (1913) along with those of *Psephurus*.

This table not only clarifies the synonymy of nomenclature, but presents also the agreements and differences in the three forms.

Acipenser (Vetter.)	*Polyodon.* (Danforth.)	*Psephurus.* (Kesteven.)
Cs.1	?	?
Cs.2 (and 6 ?)	Geniohyoideus	Csv.1
Cs.3 and 4	Not described	Csv.2
Cs.5	Not described	Interhyoideus
Add.mandibulae	Add.mandibulae	
	pars.ant.	Pterygoideus
	pars.post.	Quad.-mandib.
Protr.hyo.	Protr.hyo.	Protr.hyo.
Retr.hyom.	Retr.hyom.	Lev.hyom.
Mus.opercularis	Not described	Lev.operc.
Not described	Not described	Hyo-mandibularis
Lev.arc.br. (5)	Lev.arc.br. (4)	Lev.arc.br. (3)
Add.arc.br. (3)	Add.arc.br. (4)*	Add.arc.br. (4)
Interarc.vent. (5)	Interarc.vent. (4)	Subarc.obliqui (3)
Not described	Transv.dors.	Not found
Not described	Trans.vent.	Transv.vent.
Branch-mand.	Branch-mand.	Not found
Coraco-arc.post.	Coraco-arc.	Coraco-arc.
Coraco-arc.ant.	Pharyngo-clav.	Coraco-hyoideus
Interbranchiales	Not found	Not found

---

* Norris (1925) reports a fifth add.arc.br. in *Polyodon*.

It is probable that further examination will discover the interhyoideus and the depressor mandibulae (hyo-mandibularis) in *Polyodon*, and also that the branchio-mandibularis is really present in *Psephurus* ; maybe, I failed to find it in my young specimens on account of its tenuity.

THE CHONDROSTEI AND PLAGIOSTOMI.

Comparison of the cephalic musculature of these two groups does not involve us in much that is controversial, most of the homologies being readily recognizable. The branchial musculature does not call for analysis here.

THE HYOID MUSCLES.

Of dorsal constrictors we have only the levatores hyo-mandibularis and operculi to consider. Vetter (1878) was of the opinion that these two muscles were comparable with the superficial and deep portions of the selachian Csd.2. It will be remembered that the Csd.2, as he viewed it, included the levator hyo-mandibularis. In our study of the dorsal constrictor sheet in the Selachians we found there was a variable tendency of the most anterior fibres of the sheet to become attached below to the hyo-mandibular and posterior end of the quadrate. Further than this an intimate association of the fibres in question and the levator hyo-mandibularis was observed in the majority of the examples. In *Heterodontus* we found the most internal and anterior fibres of the sheet acting as a levator, not only in the hyoid segment but also in the branchial. In view of all these circumstances it would seem that we should agree that Vetter's comparison is correct, and that these two muscles represent the whole of the dorsal constrictor sheet of the hyoid segment.

Hyo-mandibularis. The homology of this little muscle is very doubtful. Its innervation by the hyo-mandibular ramus of the VIIth nerve indicates that it is a hyoid muscle. Its relation to the middle joint of the arch suggests the identification given in the text and table.

Protractor Hyo-mandibularis.—There is no room for doubt that in identifying this muscle with the levator maxillae superioris of the Selachians Vetter was correct. Its innervation and position alone would lead to this decision, but when, in addition, one is able to compare the muscle with the levator maxillae superioris in such forms as *Sphyrna* and *Carcharhinus*, its remarkable forward extension ceases to be a peculiar feature. The transference of its insertion to the distant end of the hyo-mandibular is an interesting example of adaptation to the requirements of the altered skeletal structures.

The identification of the anterior part of the adductor of the jaws as the pterygoideus rests upon its relation to the mandibular and maxillary rami of the Vth nerve. That relationship, however, is so very constantly maintained in all the variations of the muscle among the Selachians that the identification is made with confidence.

6. **Holocephali.** (Figs. 18-21.)

Vetter described the musculature of the head of *Chimaera monstrosa* in 1878 and I described that of *Callorhynchus antarcticus* in 1933. The cranial nerves of *C. monstrosa* were described by Cole (1896) and those of *Callorhynchus* by myself.

For the purposes of the present work I have dissected *Chimaera ogilbyi* Waite.

I reproduce, with the lettering slightly altered, my drawings of the muscles of *Callorhynchus*, and describe the muscles briefly in order that their homology with those of the Plagiostomi may be discussed.

Nomenclature and synonymy :

	C. monstrosa (Vetter.)	*Callorhynchus* (Kesteven.)	*C. ogilbyi* (This work.)
Branchial Muscles.	Interbranchiales	Obliqui ventrales	Interbranchiales
	Protr.arc.br.	Lev.arc.br.ant.	Lev.arc.br.ant.
	Not described	Lev.arc.br.post.	Lev.arc.br.post.
	Not described	Med.dors.int.obl.	Epibr.spinal
	Not described	Lat.dors.int.obl.	Obliqui dors.
	Add.arc.br.	Exter.dors.obl.	Add.arc.br.
	Cor.br.	Cor.br.	Cor.br.

	C. monstrosa (Vetter.)	*Callorhynchus* (Kesteven.)	*C. ogilbyi* (This work.)
Hyoid Muscles.	Not described	Depr.rost.et vel.	Depr.veli
	Cs.2	Lev.operc.	Csd.2b (pars arcuata)
	Hyoideus sup.	Depr.mand.sup.	Depr.mand.sup.
	Hyoideus inf.	Genio hyoideus	Interhyoideus
	Not identified	Depr.mand.sup.	Depr.mand.sup.
	Cs.4	Not identified	Not identified
	Cs.3	Post. deep constr.	Csv.2b
Mandibular Muscles.	Labialis ant.	Prot.lab.sup.	Prot.lab.sup.
		Pr.sup.lab.inf.	Prot.sup.lab.inf.
	Labialis post.	Pr.inf.lab.inf.	Csv.1a
	Cs.5	Ant. deep constr.	Csv.1b^2
	Cs.1	Supf.vent.constr.	Csv.1b
	Not present	Lev.rost.	Not represented
	Lev.ang.oris 1	Lev.lab.sup.	Lev.lab.sup.
	Lev.ang.oris 2	Lev.lab.inf.	Lev.lab.inf.
	Add.mand.	Add.man.ant.hd.	Pterygoideus
		Add.man.post.hd.	Quadrato-mandibularis
	Coraco-mand.	Cor.mand.	Cor.mand.
	Cor.hyoideus	Cor.hy.	Cor.hy.
	Trapezius	Cucullaris	Cucullaris
	Not described	Sph.oes.	Sphincter oesophagi

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

Attention is particularly drawn to the reduced interbranchial muscles. Each is a small fan of fibres with a thicker median edge. The apex of the fan is at the insertion of the muscle onto the basibranchial cartilage. The expanded upper margin is placed in the septum above the middle joint of the arch. The thicker edge, alongside of the cartilages, extends upward to an origin from the epi-branchial cartilage close to the origin of the adductor of the arch.

These reduced interbranchial muscles will be met again in *Neoceratodus* and in immature stages of the other groups of amphibians. In these latter they have been described as musculi marginales (Edgeworth, 1911, p. 232).

Only two branchial levatores are developed in each of three holocephalans which have been studied. The anterior levator arises from the ventrum of the skull in the region of the orbit; it is a narrow ribbon of muscle which passes ventrad, caudad, and laterad, to be inserted into the junction of the first and second epi- and cerato-branchial cartilages. It is innervated by the post-trematic ramus of the glossopharyngeal nerve.

The posterior branchial levator arises from the lateral edge and ventrum of the skull just behind the orbit. Its direction from origin to insertion is mediad and slightly caudad. Broader than the anterior levator, its insertion extends from the second well back across the fused third, fourth and fifth pharyngo-branchial cartilages.*

The adductores arcuum branchialium are quite typical muscles, so similar to those of the Plagiostomes that they do not call for description.

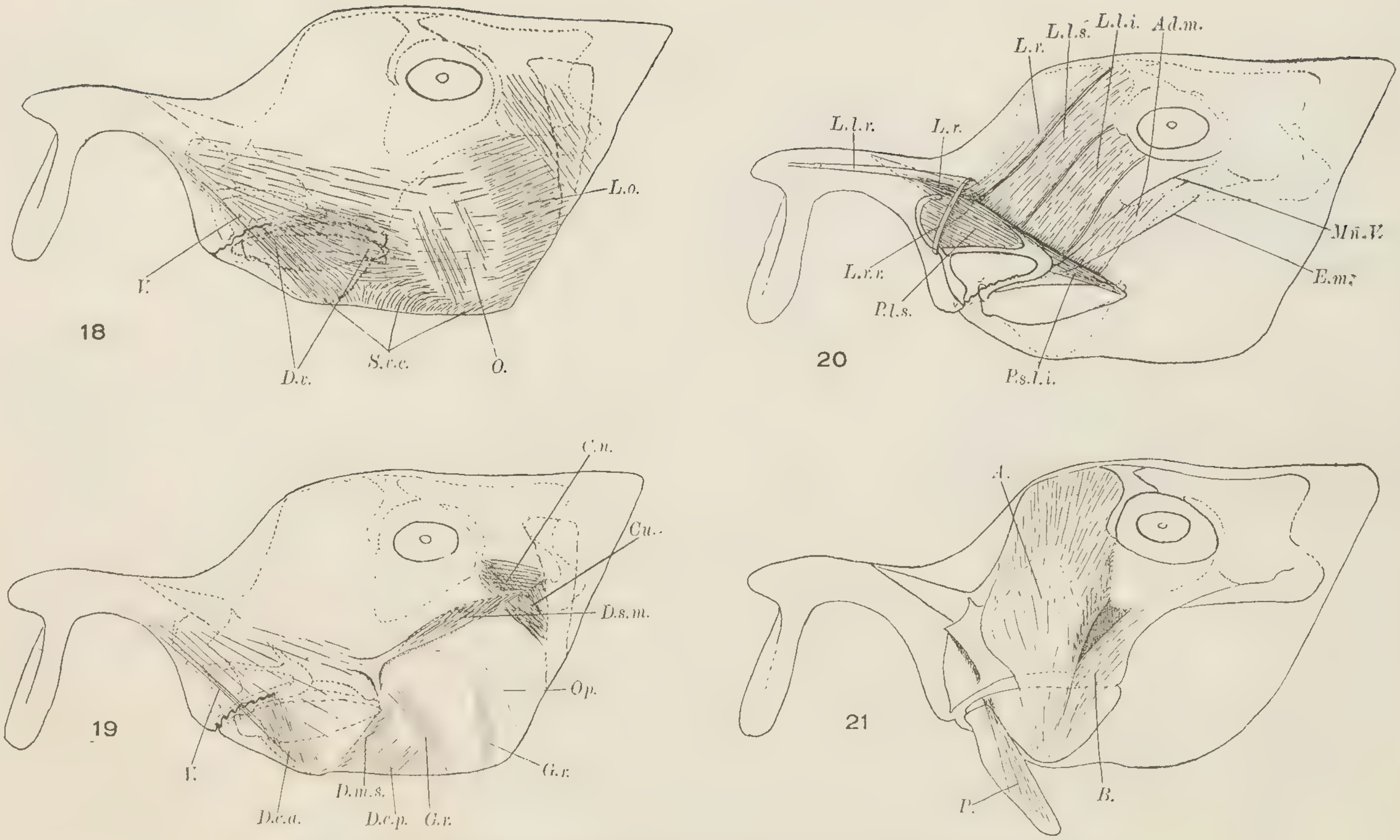
The coraco-branchialis also so closely resembles that of the Plagiostomes that it calls for no further comment.

MUSCLES OF THE HYOID SEGMENT. (Figs. 18 to 21.)

The depressor rostri et veli (Fig. 18, Csd.2) (in *Chimaera*, depressor veli only) is a very thin layer of muscle fibres which has an indefinite origin in the superficial fascia behind the jaws. Its fibres course forward and dorsad over the side of the face and have an indefinite insertion in the superficial tissues of the velum. In my account of the muscle in *Callorhynchus* I stated that it was innervated by the maxillary division of the Vth nerve. Observation of the depressor and levator rostri in batoid species leads me to think that I may have been in error in so stating. In the Batoidei the rostral muscles arise far back and, in some species, are certainly innervated by the facial nerve. In two of the species I dissected I found branches of the facial terminating by penetrating the muscle. In no species was I able to find any branch of the Vth reaching either of these muscles.

---

* It is worthy of notice that the composition of the branchial skeleton in its dorsal portion recalls strongly that of the Teleosts, especially so in the case of the fused pharyngo-branchials.


18
L.o.
V.
D.v.
S.v.c.
O.
20
L.r.
L.l.s.
L.l.i.
Ad.m.
L.l.r.
L.r.
Mñ.V.
E.m.
L.r.r.
P.l.s.
Ps.l.i.
19
C.n.
Cu.
D.s.m.
Op.
V.
G.r.
D.m.s.
D.c.a.
D.c.p.
G.r.
21
A.
P.
B.

Figs. 18, 19, 20 & 21.—*Callorhynchus.* Lateral views of successively deeper dissections (from Kesteven, 1933).

In *Chimaera ogilbyi*, as in *Callorhynchus*, I find twigs of maxillary ramus of the Vth nerve penetrating the muscle from its deep side. These twigs are quite numerous and it was assumed that some of them supplied the motor nerve for the muscle. I find, however, in both of the species, that there are also a few twigs from the external mandibular branch of the hyo-mandibular ramus of the facial which course forward over the surface of the muscle. These I now regard as the motor supply to the muscle.

The levator operculi (Csd.2b, Fig. 18), a thin sheet of muscle fibres which arises above and behind from the fascia dorsalis and runs ventrad and cephalad over the opercular membrane, and which is innervated by the external mandibular branch of the hyo-mandibular of VII, can be none other than the posterior portion of the dorsal superficial constrictor of the hyoid segment, the Csd.2b.

The ventral superficial constrictors are not readily defined from those of the mandibular segment. It seems probable that the posterior part of the superficial ventral constrictor of my description of *Callorhynchus*, and the posterior deep constrictor beneath, under cover of it (Csv.2, Fig. 19) represent the superficial constrictor of the hyoid segment. These have an indefinite origin in the superficial fascial structures over the anterior and ventral part of the opercular fold and are inserted into a median ventral raphe. Twigs from both the mandibular ramus of V and hyo-mandibular of VII can be traced into the muscle.

The interhyoideus presents an interesting condition, apparently intermediate between the protractor hyoidei of the teleosts and the interhyoideus of the plagiostomes, but, as the interhyoideus is certainly innervated by the VIIth nerve, and the protractor hyoidei by the Vth as well, we cannot be quite certain that the condition is truly intermediate.

The muscle is inserted into the fibrous investment of the symphysis of the lower jaw beneath the mucosa of the mouth. Traced back to its origin the muscle passes laterad, caudad, and slightly ventrad, to arise onto the apex of the angular expansion of the posterior border of the ceratohyal about the centre of the length of the cartilage. The muscle is ribbon-like, tapering from its tendinous origin to the broader muscular insertion, and it is innervated by a twig from the superficial internal mandibular branch of the hyo-mandibular ramus of the VIIth nerve. There is also possible an innervation by the glosso-pharyngeal nerve, but it is believed that the branch of this latter nerve which was traced to the muscle is a sensory nerve.

The depressor mandibulae superioris (Cd.2.pr., Fig. 19) is particularly well developed in *Chimaera ogilbyi*. It arises by a strong fascia from the deep edge of the lateral border of the suspensorial lamina of the skull. This fascia is attached along the full length of the lamina and is continued back behind it, attached to the fascia dorsalis, deep to the origin of Csd.2b, to gain an attachment to the pectoral arch where that lies against the trunk muscles. The muscle itself commences at the posterior end of the cranial lamina and passes forward in contact with that lamina and then passes down behind the Q-M. joint and is inserted by a fibrous ribbon into the posterior edge of Meckel's cartilage below the joint, and by an extension of the ribbon, along the inner side of the cartilage, almost to the symphysis. The posterior and deeper fibres pass more deeply and transversely, also by fibrous extension, to gain an insertion onto the inferior surface of the hypohyal, passing under the coraco-mandibularis to reach this insertion. This is apparently the hyoideus superior of Vetter.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

There is no muscle in any of the three forms studied which may be identified as a representative of the dorsal constrictor.

Csv.1a.—In *Callorhynchus* this arises from the outer surface of Meckel's cartilage at the upper margin near the anterior end and is attached to the inner surface of the posterior end of the large lower labial cartilage. In *Chimaera* there is no such cartilage developed, and the muscle is inserted into the superficial tissues of the lip near the angle of the gape.

Csv.1b (Fig. 18).—This arises in the fascial structures of the deeper layers of the velum and side of the face behind and below the mouth. It is an indefinite sheet of fibres which pass ventrad and caudad to lose their identity in the deeper layer of the Csv.2 below the inferior angle of Meckel's cartilage. The muscle is certainly innervated by twigs from the mandibular ramus of the Vth nerve and also, apparently, by twigs from the external mandibular branch of the hyo-mandibular ramus of the VIIth.

Csv.1b^2 (Fig. 18).—In view of the fact that in *Callorhynchus* the posterior fibres of this muscle are continuous with the ventral fibres of the levator operculi and the anterior with ventral fibres of the depressor rostri, this muscle might be described as a typical extra mandibularis.

The protractor labii superioris (P.l.s., Fig. 20) and protractor superior labii inferioris (P.s.l.i., Fig. 20) form a flat muscle interrupted by the posterior superior labial cartilage. It arises from the anterior upper labial cartilage and is inserted into the tissues of the lip behind the gape or into the perichondrium of the large lower labial cartilage on its outer side near the posterior end.

The levator labii inferioris (L.l.i.), levator labii superioris (L.l.s.) (and the levator rostri (L.r., Fig. 20), present in *Callorhynchus* only) are three relatively thick strap-like muscles which arise in front of one another from the crest of the skull in front of the orbit. The first is inserted into the inner surface of the large lower labial cartilage and/or the tissues of the lower lip just behind the angle of the gape. To reach this insertion the muscle passes deep to the last muscle and the small lower labial cartilage. The levator labii superioris is inserted into the tissues of the upper lip at the edge of the upper jaw, having passed deep to the upper labial cartilages to reach its insertion. The levator rostri, parallel with these two and in front of the last, is inserted into the lateral ligament of the rostrum. To reach this insertion it turns sharply forward beneath a check ligament, the ligamentum radicis rostri.

These three muscles are not fused at their contactual edges, but may be cleanly and completely separated throughout their length. All three are innervated by twigs from the maxillary ramus of the Vth nerve.

The Pterygoideus (Fig. 21).—This is the massive adductor muscle of the lower jaw. It arises from the greater part of the lateral and dorsal surface of the skull between the orbit and the nasal capsule. From this very extensive origin the fibres converge to be inserted into the outer surface of Meckel's cartilage. Innervation is by twigs from both the maxillary and mandibular rami of the Vth nerve.

The relation to the nerves is important. I quote from my description of the nerves in *Callorhynchus*: "The maxillary and mandibular rami of the fifth nerve cross the floor of the orbit below all the ocular muscles, along with the buccal division of the seventh. The trigeminal branches lie medial to the buccal nerve. As the orbit is crossed the nerves broaden out and the buccal and maxillary nerves come towards the surface, the former overlying the latter. Their situation then is upon the ribbon-like levatores of the upper and lower lips and the rostrum, and beneath the velar muscles . . . The maxillary division of the trigeminal nerve runs forward under the main stream of the buccal branches, and its terminal fibres end on the surface of the muscles beneath it. Branches to the adductor mandibulae (pterygoideus) are given off within the orbit and reach the muscle deeply. The mandibular division of the fifth nerve leaves the orbit deeply between the two heads of the adductor mandibulae muscle. (That is between the pterygoideus and the quadrato-mandibularis muscles.) It gives off a number of twigs to that muscle, some three or four of which turn downwards to supply the small posterior head of the muscle. (The quadrato-mandibularis.) The nerve comes to lie upon the same ribbon-like muscles as does the maxillary division (but low down) at the anterior end of the valley . . . and (then) continues forward to the angle of the mouth."

The quadrato-mandibularis is reduced to quite a small muscle which arises from the quadrate part of the lateral expansion of the skull behind the origin of the pterygoideus and below the orbit. It passes down and forward to an insertion on the outer surface of Meckel's cartilage behind the pterygoideus muscle.

The hypobranchial spinal muscles, coraco-hyoideus and coraco-mandibularis are typical elasmobranch muscles and do not call for further comment here.

REVIEW.

The branchial muscles depart from elasmobranch standards in several interesting features, each of which may be regarded as foreshadowing either teleost or amphibian characters.

The levator sheet is reduced to two muscles only, omitting the trapezius. These resemble so closely the levatores of the teleosts that there appears little room for doubt that the muscles are completely homologous. Each of these muscles is innervated by two post-trematic nerves (Cole, 1896, pp. 665, 667, 668, 669), the anterior by post-trematic rami from the glosso-pharyngeal and the first branchial of the vagus, the posterior by those rami from the second and third branchial divisions of the vagus. This innervation may be accepted as evidence that each is a composite muscle, and that together they represent four branchial levator muscles. The levator muscles of the Teleosts also are innervated by the branchial divisions of the IXth and Xth nerves if Herrick's observations on *Menidia* hold true for the whole class (Herrick, 1899). This would seem to clinch the case in favour of the homology of the holocephalan and teleostean branchial levator muscles, but what of the question as between the former and the selachian levatores? Here the decision is not so easily arrived at.

Lightoller asserts that the branchial levatores in the Selachians he studied are innervated by the first five spinal nerves, and these nerves, he states, also innervate the superficial dorsal constrictor muscles, these motor nerves coming from a dorso-lateral ramus of each nerve. He further states that the ventral rami of the first six spinal nerves combine to form a "large nerve trunk . . . (which) . . . proceeds caudally for a short distance to gain the space caudal to the gill basket . . . The terminal branches supply the ventral constrictors caudad to the second." Norris and Hughes (1920) omit to mention the innervation of the superficial dorsal constrictors and the levatores, but they state definitely (p. 369) that the ventral constrictors are innervated by the post-trematic rami of the branchial divisions of the Xth.

In *Pristiophorus* and in *Chiloscyllium* I found, in addition to the perforating twigs of the dorsal rami of the spinal nerves described by Lightoller, small twigs from the post-trematic rami of some of the vagal branches coursing over and ending on the medial surface of the levatores. I have been able to confirm Lightoller's observations in *Mustelus* and have not found any twigs from the post-trematic rami of the Xth related to these muscles.

In all the seven selachian types and in the five batoid types which I have dissected I have detected fine twigs from one or more of the eight post-trematic rami passing dorsad and laterad along the dorsal extrabranchial cartilage or, in its absence, the tendinous intersection which takes its place, and ending on the surface of the superficial dorsal constrictor. These I have regarded as the motor nerves to the muscles. Vetter describes the dorsal constrictor muscles as being innervated by the glosso-pharyngeal or vagus, in *Acanthias*, *Scymnus* and *Heptanchus*.

There is, then, a little doubt as to the innervation of the superficial dorsal constrictors and the branchial levatores in the Plagiostomi. If, however, we assume that the levatores are innervated by the spinal nerves and, on that account, look elsewhere for the homologues of the holocephalan and teleostean levatores we find that the only other epibranchial muscles present in the plagiostomes are the epiarcualia obliqui and the epibranchial spinal muscles, and these are both present in the Holocephali, and, moreover, the latter also are innervated by spinal nerves.

We are, therefore, compelled, per exclusionem, to conclude that the branchial levatores are homologous muscles in all three groups.

Having in mind the fact that the dorsal rami of the spinal nerves are entirely motor in character (vide Norris and Hughes), it seems certain that the twigs which Lightoller describes as reaching the levatores and dorsal constrictors must be motor nerves to these muscles. In view of the fact that the post-trematic rami are not pure motor nerves, it is not so certain that the twigs which I, and presumably Vetter, observed reaching these muscles are motor nerves. On the other hand, the innervation of the homologous levator muscles in the Holocephali and Teleostomi at least justifies the assumption that there is a double innervation of the levatores in the Plagiostomi, and that the spinal innervation has been lost by the muscles of the other groups.

The interbranchial muscles of the Holocephali are of interest, not only as foreshadowing those of the primitive and immature amphibians, but also as presenting a definite half-way stage between the fully developed muscles of the plagiostomes and their complete absence from the interbranchial septa of the teleostomes.

In the form of the epibranchial spinal, the epiarcualia obliqui and the coraco-branchialis muscles the Holocephali are typically elasmobranchian.

The peculiarly modified superficial muscles of the hyoid and mandibular segments are *sui generis*, and do not throw any light on the modifications of these muscles in the teleosts or higher vertebrates.

The interhyoideus is a particularly interesting muscle. It is quite certainly innervated by the facial nerve. Herrick (1899, pp. 157-160) discusses the genio-hyoideus and intermandibularis muscles of the bony fishes. He concludes that "the intermandibularis, genio-hyoideus and hyo-hyoideus of ganoids and teleosts have unquestionably been derived from this ventral constrictor system of the selachians " innervated by the Vth and VIIth nerves. After discussing an ill-founded assumption by Rudge (1897) that the muscles are innervated by the VIIth nerve in all forms by anastomosis, peripheral or intracranial, he states : " In *Menidia*, at any rate, it is clear the exact reverse is true, the apparent innervation by the facial in reality being derived from the motor nucleus of the trigeminus, as there is no possible opportunity for a confusion at any point between the motor fibres of the V and VII nerves ". Vetter found the genio-hyoideus in *Esox* to be innervated by the facial, and Herrick confirmed this observation in *Gadus* (l.c., p. 157). In both these instances and in *Amia* (Allis, 1897) the innervation by the facial is by a branch which communicates with the trigeminus. From this Herrick infers that " in forms like *Esox*, in which the so-called genio-glossus (genio-hyoideus) is innervated from both V and VII nerves we may assume that the muscle represents both facial and trigeminal constrictor systems, comparable with those of *Ceratodus*, while in *Menidia* and most other teleosts the VII portion has been lost and the muscles ' genio-hyoideus ', together with the intermandibularis, represent the ventral constrictor muscles of the ' trigeminus ' segment, the facialis constrictor muscles being represented only by certain dorsal opercular muscles and by the branchiostegal muscles ".

The interhyoideus of the Holocephali differs from the similarly-named muscle in the Plagiostomi in arising from the fibrous investment of the symphysis of the lower jaw, deep to the insertion of the coraco-mandibularis instead of from the deep surface of the median ventral fascia superficial to that insertion.

Unless we are to regard it as an entirely new development, without any homologue among the muscles of the plagiostomes, we are forced, once again per exclusionem, to homologize the two muscles notwithstanding this difference. If we accept this identification we assume that the hypobranchial spinal muscles grow forward between the deep and superficial ventral constrictors instead of, as in the plagiostomes, deep to them both.

The assumption appears reasonable.

In 1910 Holmqvist described " many varieties of the interhyoideus and protractor hyoidei of the teleostei ". Unfortunately I have not been able to consult this work, but Edgeworth (1928, pp. 61-63) briefly reviews it and adds brief descriptions of the muscles in several bony fishes. He asserts that, " the Protractor hyoidei of many teleostei is a compound muscle, being an Intermandibularis posterior plus Interhyoideus ", and the assertion is based on sound embryological evidence.

It may finally be concluded that the interhyoideus muscle of the Plagiostomi and of the Holocephali are homologous muscles and that the protractor hyoidei of the Teleostomi is derived, in part, at least, from this muscle.

The return to a superficial position, which the muscle occupies in the bony fishes, is due to the fact that the hypobranchial spinal muscles do not extend forward to gain an insertion onto the mandible.

The depressor mandibulae superior. This muscle also is of particular interest. It is unquestionably derived from the anterior portion of the hyoid dorsal constrictor, the Csd.2.pr, and probably also the closely related hyoid levator of the plagiostomes. The particular interest attaching to the muscle is that it appears to confirm in part, at least, Lightoller's statement that the depressor mandibulae of the Axolotl " is a composite muscle and represents the second levator and the pars quadrate-hyoidea of the Elasmobranchei ". There is reason to believe that no IXth nerve components supply motor elements to the muscle in any of the Amphibians. Norris describes, in *Siren* (1913, p. 296) and Norris and Hughes (1918, p. 527) in the Caecillians, unmixed innervation by VII.

Any attempt to determine the homology of the muscle formed by the protractor labii superioris and the protractor superior labii inferioris, in the present state of our knowledge must be based on their innervation alone. Obviously they belong to the mandibular segment, for very definitely they are innervated by the Vth nerve.

The three levatores of the lips and of the rostrum are in much the same case. We observe, however, that the levator maxillae superioris, so constantly present in the plagiostomes, is apparently missing from the holocephalan head. As developed in such forms as *Mustelus Chiloscyllium* and *Heterodontus*, there is little in common between the lev.max.sup. and the muscles we are considering, but in *Sphyrna* and *Carcharhinus* we find the maxillary levator arising from an extensive area of the side wall of the skull between the orbit and the nasal capsule.

The resemblance in origins in these examples might suggest homology with the holocephalan muscles.

On the other hand, the levator maxillae superioris lies, always, caudad or superficial to the R. maxillaris V, whilst these holocephalan muscles lie rostrad and deep to that nerve. The development of the levator maxillae superioris from the upper portion of the mandibular muscle plate appears to render it quite impossible that the muscle should acquire a situation rostrad and deep to this nerve. For the present, the most that can be said is that these muscles are derived from the same part of the muscle plate as the pterygoideus.

The pterygoideus. That this is the homologue of the pterygoideus of the plagiostomes seems to be quite satisfactorily proven by its relation to the mandibular and maxillary rami of the Vth nerve, and by a comparison with the pterygoideus muscle in *Chiloscyllium.*

The quadrato-mandibularis muscle lying behind the pterygoideus, with the nerve between them, is very much reduced and would appear to represent the pars posterior only of the plagiostome muscle.

It will be noted that in these last two muscles the Holocephali again present resemblances rather to the Amphibia and Teleostomi than to the rest of the Elasmobranchii.

From the foregoing review it is apparent that in their epiarcualia obliqui, epibranchial spinal, coraco-branchialis and hypobranchial spinal muscles the Holocephali are essentially elasmobranchial in character. In the form of the branchial levatores, the levator operculi and the interhyoideus they resemble the teleosts. In the form of the interbranchial muscles, the adductors of the jaws and the depressor mandibulae they resemble the amphibians.

The resemblance in origins in these examples might suggest homology with the holocephalan muscles.

On the other hand, the levator maxillae superioris lies, always, caudad or superficial to the R.maxillaris V., whilst these holocephalan muscles lie rostrad and deep to that nerve. The development of the levator maxillae superioris from the upper portion of the mandibular muscle plate appears to render it quite impossible that the muscle should acquire a situation rostrad and deep to this nerve. For the present, the most that can be said is that these muscles are derived from the same part of the muscle plate as the pterygoideus.

The pterygoideus. That this is the homologue of the pterygoideus of the plagiostomes seems to be quite satisfactorily proven by its relation to the mandibular and maxillary rami of the Vth nerve, and by a comparison with the pterygoideus muscle in *Chiloscyllium*.

The quadrato-mandibularis muscle lying behind the pterygoideus, with the nerve between them, is very much reduced and would appear to represent the pars posterior only of the plagiostome muscle.

It will be noted that in these last two muscles the Holocephali again present resemblances rather to the Amphibia and Teleostomi than to the rest of the Elasmobranchii.

From the foregoing review it is apparent that in their epiarcualia obliqui, epibranchial spinal, coraco-branchialis and hypobranchial spinal muscles the Holocephali are essentially elasmobranchial in character. In the form of the branchial levators, the levator operculi and the interhyoideus they resemble the teleosts. In the form of the interbranchial muscles, the adductors of the jaws and the depressor mandibulae they resemble the amphibians.

THE MUSCLES OF THE BONY FISHES.

The whole of the teleostomes are, in their cephalic musculature, essentially similar. There are differences between individual members of the Teleostei as great as those between them, as a group, and *Polypterus* and/or *Lepidopterus* and *Amia* ; nor, with the possible exception of the branchio-mandibularis muscle, are such differences of a more significant character.

TELEOSTOMES.

		Branchial Segments.	Hyoid Segment.	Mandibular Segment.
Superficial constrictors	Dorsal ..	Absent	Lev.operc.hyohyoideus	Absent
	Ventral	Absent	Hyohyoideus Protractor hyoidei	Submentalis Interm.post.
Deep Constrictors	Dorsal ..	Absent	Absent	Dil.operc.
	Ventral ..	*Subarcualis transv.	Absent	Absent
Levators		Lev.arc.branch	Add.arc.pal., Add.hyom., Add.operc.	Lev.arc.pal.
Epibranchial Spinal Muscles ..		Retr.dors.arc.br.	Absent	Absent
Adductor Muscles	Dorsal ..	Epiarc.obliqui, transversi and recti	Absent	Pterygoideus
	Middle ..	Add.arc.br.	Absent	Temporomassetericus
	Ventral ..	*Subarcualia obl.	Absent	Absent
Ventral Interarcual Muscles ..		*Subarcualia recti	Absent	Absent
Depressors		Claviculo-branch.	Absent	Absent
Hypobranchial Spinal Muscles		Claviculo-hyoideus	Genio-hyoideus	Absent

* These muscles are derivatives of, or substitutions for, the interbranchialis muscles of the Plagiostomes. They develop from the deep portion of the primordial muscle plate.

Material.—One specimen of *Polypterus* (*senegalus* ?).* Several heads of *Amia* and of *Lepidosteus osseus* and *platystomus*. Among modern teleosts I have dissected *Platycephalus fuscus* Cuv. and Val., *Mugil cephalus* Linné, *Girella tricuspidata* Quoy and Gai., and *Anguilla reinhardti* Stdr. Of these four species I have had many specimens, the four fish being very common. In addition I have had one or more specimens of the following, and all have been more or less completely dissected and studied : *Epibulus insidiator* Pallas, *Drepanichthys punctatus* Linné, *Zanclistius elevatus* Ramsay and Ogilby, *Cantherines ayraudi* Q. and G., *Gonorhynchus greyi* Rich., *Fistularia petimba* Lacep., *Hemirhamphus intermedius* Cantor, *Balistapus aculeatus* Linné, *Tandanus tandanus* Mitchell, and *Cnidoglanis megastomus* Rich.

For most of this last group of species my thanks are tendered to the Trustees of the Australian Museum and to Mr. G. P. Whitley.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

There are neither superficial nor deep constrictor muscles present in the branchial segments of any of the teleostomes.

It is very doubtful whether the epibranchial spinal muscles of the elasmobranchs are developed in the bony fishes. Edgeworth (1911, p. 266) discusses the "Muscles Derived from Trunk Myotomes Passing to the Upper Ends of the Branchial Bars". He confirms Furbringer's observations (1897) as to the origin of these muscles in the Elasmobranchs and their innervation by occipito-spinal nerves, and further asserts that the retractor arcuum branchialium dorsalis of Teleosts has similar origin in *Amia* and in *Lepidosteus*. In view of the fact that, for the purposes of the work quoted from, Edgeworth studied the development of the muscles of those two forms and also of *Salmo*, it would appear that this is the only spinal epibranchial muscle in the teleosts. In *Scyllium* these epibranchial muscles are developed from the first to the fourth spinal myotomes. In *Amia* the muscle is developed from the sixth to the thirteenth, and in *Lepidosteus* from the third to the ninth trunk myotomes (vide Edgeworth), therefore, though of similar origin, it is doubtful whether it is strictly homologous with the spinal epibranchial muscles of the Elasmobranchii.

The branchial arches of the Teleosts are, when compared with those of the Elasmobranchs, crowded together under the cranium and they have become extensively fused dorsally. We have seen this crowding initiated in the Holocephali and have observed it to be accompanied by a suppression of the superficial constrictors, a marked reduction in the size of the deep constrictors, and a reduction in the number of the branchial levators. In the Teleosts the crowding is more pronounced, and is accompanied by a suppression of the deep constrictors as well as of the superficial ; the levators, on the other hand, are not so reduced in number, whilst the other branchial epibranchial muscles present not only greater development, but also an increase in number and in diversity of form.

In the result we have, in addition to the levators, the following dorsal branchial muscles to describe : epiarcualia obliqui, epiarcualia transversi and epiarcualia recti.

Adductores arcuum branchialium are present and are quite similar to those of the Elasmobranchs.

There is also a striking increase in the number and variety of ventral branchial muscles. In addition to the depressors, and the coraco-branchialis, there are also subarcualia obliqui, subarcualia transversi and subarcualia recti.

Edgeworth (1911) reserves the term "hypobranchial cranial" for the coraco-branchialis and its homologue the pharyngo-clavicularis. He states that, in the Teleostomi, in branchial segments where these muscles are not formed there is a downward and inward growth of the ventral ends of the branchial myotomes to form the lower portions of the obliqui ventrales (subarcuales obliqui). He further states that the portions of the branchial myotomes next above the "anlagen" of the coraco-branchialis form the upper portions of the subarcuales obliqui in teleostoman embryos, and that these may or may not unite with the lower portions. In a later work (1928) describing the development of some of the cranial muscles of Ganoid Fishes, including *Acipenser*, he demonstrates that from the ventral end of a branchial muscle plate there may develop any one of the three forms of ventral branchial muscle met with in the Teleosts, and further, that an originally single transversus ventralis (subarcualis transversus) may split, in later embryonic stages, into a subarcualis transversus and subarcualis obliquus, and, finally, that the oblique muscle "may be formed either from a fully developed transversus, i.e., from one which meets its fellow in the midline . . . or from an incomplete one, i.e., from one which passes inwards towards but does not actually join its fellow."

---

* This was a young specimen 50 mm. in length, which I received from Prof. Graham Kerr, to whom my grateful thanks are tendered. The specimen was divided in halves along the mid-sagittal plane. Both halves were stained with carmine and picric acid ; one was dissected under a Greenough binocular dissecting microscope, the other was cut into serial sections parallel to the plane of division. For the sectioning of the specimen and its mounting I have to thank Prof. C. W. Stump.

It will be remembered that the deep branchial constrictor (interbranchial muscle) of the Elasmobranchs is developed from that portion of the branchial muscle plate which lies between the "anlage" of the coraco-branchialis below and the adductor arcuum branchialium and epiarcualis obliquus above. In short it is developed from the same portion of the plate as the intrinsic ventral branchial muscles are developed in the Teleosts.

These muscles, therefore, truly replace the interbranchial muscles of the Elasmobranchs, having with them a common origin, and to this extent they may be regarded as homologous.

The following description of the muscles is based largely on the dissections of *Platycephalus*, *Anguilla* and *Girella* supported by notes and comparisons on other forms where called for.

THE LEVATORES ARCUUM BRANCHIALIUM.

Of these there are, commonly, four developed, but the first two or three may divide longitudinally, giving rise to internal and external portions which, in the adult, are described as separate muscles.

Platycephalus.—There are five branchial levators present. Four of these arise close together, medial to and behind the cranio-hyomandibular articulation, from the ventral surface of the pterotic bone. Of these four, two are internal and two external levators, and corresponding relation one to the other is found at their origin. The two external are in line immediately next the hyomandibular face and the other two in line medial to them. The general direction of the four from their origin is mediad, caudad and slightly ventrad. The first internal levator is inserted onto the anterior margin of the os pharyngeum superior.* The second internal is inserted onto the same bone further back, medial to the articulation of the second infrapharyngobranchial. The first external levator is inserted onto the anterior surface of the first infrapharyngobranchial just above its attachment to the epibranchial. The second external levator is inserted into the tip of the fourth epibranchial and by a small slip of muscle and a fine tendon, forming an anterior head, into the third epibranchial cartilage as well. The fifth levator belongs to the external series. It arises, at some distance from the others, from the extreme postero-lateral corner of the pterotic bone and passes ventrad direct to its insertion onto the tip of the fourth epibranchial cartilage lateral to the insertion of the second levator.

Anguilla.—Here also there are five levatores arcuum branchialium. Of these, four may be described as external and one only as internal. The levator of the first arch arises from the periosteum of the suboperculum. The point of origin is far up near the dorso-posterior tip of the bone on its inner surface. From this origin the muscle passes caudad, and slightly ventrad and laterad, to be inserted on the dorso-medial edge of the first epibranchial just above its joint with the ceratobranchial. The second, third and fourth levators arise close together from the base of the skull medial to and in front of the hyomandibular joint. They are inserted into the second, third and fourth epibranchials, precisely as is the first. The fifth arises medial to and below the other three and passes back nearly parallel to the others but medial and ventral to them, to be inserted onto the capsule of the joint between the epi- and pharyngo-branchials of the third arch. This is apparently the only internal levator of the series.

Mugil, Tandanus and Cnidoglanis.—In these three also I find but five levators, and their origin and insertions are little different from those described in the preceding two genera.

Epibulus.—Here there are six levators inserted in line one behind the other along the outer edge of the dorsum of the branchial basket. Of these the anterior four arise together just behind and medial to the hyomandibular facet. They are inserted into the epibranchials of the first four arches just above the joints with the ceratobranchials. The posterior two external levators arise from the postero-lateral corner of the inferior surface of the skull just medial to the cranial attachment of a very strong cranio-scapular ligament. They pass ventrad and slightly laterad to be inserted onto the outer ends of the fourth and fifth epibranchials. The more posterior of these two is carried ventrad behind the fifth epibranchial by a fine tendon which is attached to a posteriorly and ventrally directed spur of the ceratobranchial of the same arch. There are also two internal levators. These arise in company with the anterior external levators and are inserted into the pharyngobranchials of the second and third arches.

---

* The os pharyngeum superior in *Platycephalus* is formed by the fusion of the pharyngobranchials of the second, third and fourth arches, as far as one may judge by the adult conditions.

Girella.—This genus was found to have the levators arranged exactly as described by Allis (1903) in his account of the anatomy of the head of *Scomber.*

The Ganoids.—The levators of the Ganoids have been described by Allis. Those of *Amia* are essentially similar to those of *Epibulus*, *Girella* and *Scomber*. The fifth external levator is inserted onto the fourth arch as in *Epibulus* and is also continued ventrad to an insertion onto the fifth ceratobranchial and, finally, as in *Scomber* and *Girella*, is further attached to the clavicle. There is no sixth external levator present. In *Polypterus* there are only five branchial levators. Of these the first is inserted into the junction of the first pharyngo- and epibranchials, the second and third into second and third pharyngobranchials and the fourth into the tip of the fourth ceratobranchial. The fifth is inserted into the clavicle.

Innervation.—These muscles are innervated by branches of the post-trematic rami IXth and Xth nerves.

DISCUSSION.

The levatores arcuum branchialium in the bony fishes are, in the various genera, variable in number, site of origin, and insertion. It may be said of them (1) that they vary in number from five to eight, (2) that they arise from the inferior surface of the skull in the neighbourhood of the hyomandibular facet, medial to the origin of the levator and adductor muscles of the operculum, (3) that commonly several arise close together in this situation, (4) that usually one or more arise further back at a little distance from the anterior group, (5) that the anterior one, two or three pairs are developed from single muscles, (6) that the internal levators are inserted into pharyngobranchials, or pharyngoepibranchial junctions, (7) that the external muscles are inserted into the epibranchials in proximity with the epi-ceratobranchial joint, (8) that the most posterior of these levators may be inserted into the clavicle and not into a branchial element.

Edgeworth (1911, pp. 239, 241, 291) regards this last as a reduced trapezius (see also Straus and Howell, 1936).

THE EPIBRANCHIAL SPINAL MUSCLES (RETRACTORES DORSALES ARCUUM BRANCHIALIUM).

Apparently there is never more than a single pair of these muscles developed in any of the bony fishes. In the great majority the muscles arise from the side of the first one or two vertebrae, in some forms reaching as far back as the third. Normally it is a flat ribbon-like muscle which passes forward from its origin nearly horizontally to an insertion onto the posterior margin of the branchial skeleton in front of the posterior transverse epiarcual muscle. The actual element on which the muscle is inserted is apparently determined to some extent by the degree of divergence of the dorsal branchial members from in front caudad. Where there is a more or less closed posterior angle between the posterior arches dorsally the insertion is onto the fourth or fifth epi- or pharyngobranchial, but where this angle is more open the insertion may be onto the third or even the second pharyngobranchial, in front of the anterior transverse muscle.

The width of the muscle varies greatly, and in some forms, e.g. *Girella*, the muscle is a relatively thin rounded cord-like strand. In most cases there is no fusion with any other muscle, but in *Amia* and in *Platycephalus* the muscle is broad and fuses anteriorly with the anterior transverse muscle and with its own antimere.

Anguilla is quite peculiar ; in this form the muscle is a quadrangular sheet of muscle fibres which arise from the fascia dorsalis immediately under cover of the anterior portion of the origin of the hyo-hyoideus and, curving ventrad in contact with the trunk muscles, is inserted into the tip of the first and along the median edge of the second pharyngobranchial, and by a fine membranous extension onto the third pharyngobranchial. This membranous extension arches over the internal levator and passes laterally to the branches of the vagus nerve and to the anterior tributaries of the dorsal aorta, and then curves slightly mediad below them to the insertion.

THE EPIARCUALIA OBLIQUI (OBLIQUE DORSALES) AND EPIARCUALIA RECTI (INTERARCUALES DORSALES).

Doubtless these are but forms or extensions of the one variety of intrinsic dorsal branchial muscle of the Elasmobranchs. The term "interarcual" has been discarded for the more explicit designations above. The "obliqui" are those muscles whose origin and insertion are both on elements of the same arch, whilst the "recti" are those whose origin on one and insertion on another arch would entitle them to the designation interarcual had not this term already been used to indicate both varieties.

The recti vary in number from one to three. In *Platycephalus* there is but one, which arises from the anterior and medial curved margin of the os pharyngeum superior. At its origin the muscle is relatively thick and flat, but becomes narrowed and nearly cylindrical as it passes caudad and laterad to be inserted into the dorsal end of the fourth ceratobranchial, just where that is attached to the third. In *Anguilla* there are two epiarcualia recti. The first is a very short little muscle which arises from the dorsal end of the fourth epibranchial and is inserted into the third pharyngobranchial. The second is equally small and partly fused with the second obliquus. It arises from the fifth ceratobranchial and is inserted in front of the second obliquus onto the os pharyngeum superior. Allis, who (1903) designates them interarcuales dorsales, describes three in *Scomber*. In *Amia* Allis (1897) describes two obliqui dorsales which pass from an element of one arch to an insertion on another arch, and would therefore fall within the present group.

The epiarcualia obliqui are more variable in number. In *Platycephalus*, as in *Amia*, there are no epibranchial muscles which arise from and are inserted onto elements of the same arch. In *Anguilla* there are two of these muscles. The first arises from the epibranchial and is inserted into the pharyngobranchial of the third arch, the second arises from the epibranchial of the fifth arch and is inserted into the os pharyngeum superior. In *Scomber*, Allis describes three epiarcualia obliqui.

In *Lepidosteus* there are neither epiarcualia obliqui nor recti.

EPIARCUALIA TRANSVERSI.

There are apparently always two of these muscles present in the Teleostome, excepting only *Lepidosteus* in which neither of the two is present.

In *Platycephalus* the anterior transverse epiarcual muscle is a thin sheet of fibres which takes origin on each side from the first and second infrapharyngobranchial and is inserted into a median aponeurosis. The posterior margin of the muscle lies dorsally to the origin of the epiarcual rectus. The posterior transverse arises from the fourth epibranchial and posterior edge of the os pharyngeum superior and, passing horizontally mediad, becomes continuous with its antimere. The retractor dorsalis arcuum branchialium passes forward to its insertion in contact with the ventral surface of this muscle, separating it very completely from the sphincter oesophagi.

In *Anguilla* the anterior transverse muscle lies between the two third arches. The posterior transverse is intimately fused with the sphincter oesophagi.

In *Scomber*, Allis describes both muscles.

In *Amia* both muscles are present.

Unfortunately we have little exact knowledge about the development of the dorsal branchial muscles. The most important contributions known to me are those of Edgeworth. It would appear that they are all developed from that portion of the branchial muscle plate which, in the Elasmobranchs, gives rise to the epiarcualia obliqui only, and that two or more of these teleostoman forms of branchial epibranchial muscles may be developed from a single primordium. Further, it appears that the muscle or muscles developed from this primordium may grow forward or backward to gain attachments to arches in front of or behind that to which the muscle-plate properly belongs.

It follows from the foregoing that we must homologize all these three varieties of dorsal branchial muscle with the single form we are familiar with in the Elasmobranchs. It also follows that the numerical identification of any muscle related to more than one arch, unless it be obviously portion of an oblique muscle, will rest upon its innervation; and that, if there be a dual innervation, its developmental history alone will decide the question as to whether it be two muscle-plate derivatives fused, or a single derivative which has acquired a secondary motor innervation.

THE ADDUCTORES ARCUUM BRANCHIALIUM.

These do not call for extended description; when present, they are always essentially the same. Each arises from the posterior, and upper, end of a ceratobranchial and is inserted into the epibranchial close to the joint with the former. The muscle is always short and relatively stout and it lies anterior and medial to the joint.

The number of these muscles which may be present varies from five to three, the last two may, as in *Platycephalus*, be more or less completely fused at their origin.

In the Elasmobranchs, Edgeworth does not regard the fifth of this series as being homologous with the others, because, whereas they are developed from the branchial muscle plates, this is developed from the constrictor oesophagi which in turn is developed from the splanchnic mesoblast and is therefore not a branchial muscle.

In the Teleosts, however, a muscle very similar to the constrictor, but developed from the fifth branchial muscle plate, takes its place; this Edgeworth designates the Sphincter oesophagi (1928, pp. 76-77).

In the work just referred to, Edgeworth draws a distinction between the adductores arcuum branchialium of the Elasmobranchs and those of the bony fishes on account of certain features in their development and a difference in the course of the motor nerve to the muscles in the two groups. He would not regard the adductors in the groups as homologous series, and proposes to designate the muscles in the Ganoidei "attractores". Whilst not even implying any inaccuracy in his observations, it does not appear reasonable to regard these muscle series as other than homologous. That they are developed in slightly different manner in the two groups may well have come about directly, without, as his view implies, the suppression of the primitive adductor and its replacement later by another muscle. This latter would involve us in the further assumption that an adductor was absent from one phylogenetic stage, unless it be assumed that the later muscle dispossessed one already in possession of the site.

The case of the fifth adductor in the Elasmobranchs is different. It is not at all unreasonable to assume that the massive constrictor primordium and, later, the muscle itself, had extended its attachment along the margin of the fifth arch and displaced and finally quite usurped the situation and function of the small branchial derivative. There is no discontinuity involved in the assumption.

VENTRAL BRANCHIAL MUSCLES.

THE SUBARCUALIA OBLIQUI, TRANSVERSI AND RECTI.

That these three forms of intrinsic ventral branchial muscle develop from a common primordium has already been stated. They are numerically as variable as the dorsal branchial muscles. In *Amia* there are four oblique ventral muscles, the fourth being that which Allis designated the obliquus ventralis IV^1, two subarcualia recti, the muscles which Allis designated obliqui ventrales IV^2 and IV^3, and two subarcualia transversi. In *Platycephalus* I find a single obliquus, a single rectus and two transversi. In *Anguilla* there are a single rectus, three obliqui and two transversi. In *Scomber* Allis described no subarcualia recti, two obliqui and two transversi. *Polypterus* is of interest as presenting, in the adult, traces of the origin of the muscles. Edgeworth has studied the development of the muscles in *P. senegalus*. There are two recti and three obliqui. Rectus and obliquus 1 are developed from the first branchial muscle plate. Obliquus 2 almost joins its antimere to form an anterior transversus medially, and laterally it is partially fused with the first rectus. The muscle derived from the third muscle plate remains as a simple obliquus, that from fourth muscle plate becomes a rectus and grows forward to become attached to the second arch. There are only four arches in *Polypterus* and we have here all four muscle plates represented. There is, in addition, a posterior transversus which is developed from the fourth muscle plate.

Edgeworth regards the subarcualis transversus as more primitive than the obliquus; he tabulates the latter as being developed from the former, and we have, in a previous page, quoted his statement to the effect that an obliquus may be developed from a fully formed or from an incomplete transversus.

Since the branchial muscle plates are not primarily joined one to the other ventrally, it would appear more in keeping with their history to regard the oblique as the primitive form and the temporary ventral union, observed in some instances, as an abortive attempt to form a transversus.

THE BRANCHIAL DEPRESSOR MUSCLES.

The muscle which we know as the coraco-branchialis in the Elasmobranchs has been designated the pharyngo-clavicularis by Allis. Edgeworth, however, applies the one name to the muscle in all the fishes.

It would appear that only two portions, at most, of the quinquepartite muscle of the Elasmobranchs are developed in the bony fishes. It is proposed here to recognize the development of the clavicle on the pectoral girdle and to designate the muscles claviculo-branchialis internus and externus, remembering, of course, that each is paired.

The claviculo-branchialis internus in *Platycephalus* is a relatively large spindle-shaped muscle which arises by a fine tendon from the mesial edge of the anterior end of the fifth ceratobranchial, beneath the posterior margin of the anterior subarcual transverse muscle and between the origin of the posterior transverse muscle medially and that of the external claviculo-branchialis laterally. From this origin the muscle passes, horizontally, caudad and slightly laterad, to be inserted by another fine tendon into the lateral edge of the clavicle near its dorsal limit. The tendon of insertion lies against the lateral surface of the anterior pectoral muscle medially and the postero-median wall of the fifth branchial cleft laterally.

The claviculo-branchialis externus is a short quadrilateral sheet of muscle fibres, of no great thickness, which arises from the dorso-lateral edge of the clavicle above the anterior limit of the origin of the anterior pectoral muscles, and passes directly dorsad to be inserted into the inner edge of the ventral surface of the fifth ceratobranchial along the anterior quarter of the length of the bone.

In *Anguilla* there is only the claviculo-branchialis externus. This is a relatively massive muscle which arises from the lateral surface of the clavicle along the greater part of its length. The most anterior fibres of the muscle pass cephalad and slightly dorsad to be inserted into the fifth hypobranchial, the most posterior pass almost directly dorsad to be inserted onto the ventral surface of the fifth ceratobranchial. The intermediate fibres are inserted onto the whole of the length of the interior surface of the cerato- and basi-branchials between the two limits. The posterior limit is about one-third of the length of the bone from its posterior end.

Scomber and *Amia* are intermediate in condition between *Anguilla* and *Platycephalus*, *Amia* approaching the more nearly to the conditions in *Platycephalus*.

In *Polypterus* there is but a single muscle, as in *Anguilla*. Allis finds that it is possible to separate the muscle into anterior and posterior parts at its insertion. The latter is said to be inserted on to that part of the fourth arch which corresponds to the hypobranchial, the other on the portion which corresponds to the ceratobranchial. This separation is most marked in *P. bichir* and least so in *P. ornatipennis* (Allis, 1922, p. 259).

Although reduced in number of component parts, there is no room for doubt that these two muscles are completely homologous with the corresponding components of the elasmobranch coraco-branchialis. That this is so is made abundantly clear by the work of Edgeworth on the development of the muscles in the Ganoids (1928) and Elasmobranchs (1926).

It is not without interest to note that the division of the muscle into partes internus (medialis) and externus (lateralis) is foreshadowed in the batoid Elasmobranchs (see antea, p. 36).

THE PHARYNGO-HYOIDEUS.

This very misleading name is bestowed by Allis upon a muscle which arises from the bone which he designates " sternum " and Vetter " urohyal ", and which is inserted on to the fifth ceratobranchial. For reasons set forth elsewhere I have designated the bone in question " infrabasibranchial ".

Actually the muscle has neither origin nor insertion on any part of the hyoid arch, and is in all probability one of the subarcualia recti. It is not found in the absence of the infrabasibranchial.

In *Platycephalus* the muscle arises from the anterior third of the dorsal edge of the dorsal ridge of the bone, sharing this portion of the ridge with its antimere. From its origin the muscle passes caudad and slightly dorsad and laterad, to be inserted by a fine tendon onto the inferior surface of the fifth ceratobranchial about one-third of the length of the bone from its posterior end. At its origin the muscle is flat, but it becomes nearly cylindrical just behind the posterior limit of the origin. The fibres are inserted into a tendinous sheath which covers the lateral surface of the muscle ; posterior to the insertion of the fasciculi the tendon is continued caudad for a distance equal to half the length of the fleshy part of the muscle.

Innervation.—This is from the post-trematic ramus of the first branch of the vagus.

The muscle in *Scomber* (*fide* Allis) is very similar ; it is innervated by a twig from the post-trematic ramus of the second division of the vagus, and perhaps also by a similar twig from the fourth division.

HYPOBRANCHIAL SPINAL MUSCLES.

THE GENIO-HYOIDEUS (S. BRANCHIO-MANDIBULARIS).

This muscle was designated branchio-mandibularis by Allis, who adopted the name from Vetter. Edgeworth has studied its development not only in the bony fishes but also in the Elasmobranchs and in several Amphibians, as well as in the Rabbit. From his work it appears quite clear that the muscle is completely homologous with the genio-hyoideus of the Amphibia and with the anterior portion of the coraco-mandibularis of the Elasmobranchs. I have adopted Edgeworth's designation for the muscle.

The genio-hyoideus is found, amongst the Teleosts, only in *Amia, Lepidosteus, Polypterus* and, probably, in *Calamichthys.* It is also present in all the Chondrostei.

It is a small muscle which arises from the mandible on either side of the symphysis, and passes caudad to be inserted onto the third ceratobranchial or basibranchial.

Innervation.—This is by a twig from the occipito-spinal ventral trunk.

THE CLAVICULO-HYOIDEUS.

This is a massive muscle, usually more or less completely fused along the mid-line with its antimere, which arises from the greater part of the ventral surface of the clavicle. From this extensive origin the muscle passes cephalad, tapering rapidly, to be inserted onto the hypohyal. When an infrabasibranchial is present the muscle is inserted onto both dorsal and ventral surfaces of that bone, surrounding it almost completely. The attachment to the hypohyal, however, is still provided for by the two very strong ligaments that bind the antero-lateral corners of the infrabasibranchial to the hypohyals.

Not uncommonly this muscle is quite inseparable from the anterior pectoral muscles at its origin.

Innervation.—This is by the occipito-spinal nerves.

This muscle is completely homologous with the coraco-hyoideus of the Elasmobranchs, but it seemed advisable to recognize, in its designation, that the clavicle is present in the place of the coracoid, as was done in the designation of the claviculo-branchialis.

THE CONSTRICTOR MUSCLES OF THE HYOID AND MANDIBULAR SEGMENTS.

We have already noted that the ventral constrictors of these two segments are, in certain Teleosts, so fused as to render a study of their development in every form necessary before it were possible to state where the one begins and the other ends. The dorsal constrictor of the hyoid segment is continuous with the ventral, and it therefore becomes necessary to treat together the derivatives of the elasmobranchian Csv.1, Csv.2, and Csd.2.

THE SUBMENTALIS MUSCLE AND THE INTERMANDIBULARIS POSTERIOR.

These muscles have variously been designated by previous writers. Each is, however, homologous with only portion of the Csv.1 of the Elasmobranchs and to that extent the use of the name intermandibularis for either is misleading. On the other hand one is probably completely homologous with the submentalis of the Amphibia and higher vertebrata.

Platycephalus.—The intermandibularis posterior (Csv.1*a*) is exposed by the removal of the skin. It is composed of two small triangular, thin sheets of muscle, each of which arises from a short line along the inner surface of the dentary. This line commences just a little behind the symphysis. The posterior few bundles of fibres of the two sheets are quite continuous across the mid-line, but in front of these the fibres become successively shorter, the most anterior hardly extending far enough to appear medial to the slight " overhang " of the dentary. In the result there is left between and in front of the two muscle sheets a fine but strong fibrous sheet, which is attached to the dentary bones in continuation of the line of origin of the muscle right forward to the symphysis.

The line of origin of the muscle is not immediately deep to the skin. There intervenes between the skin and the muscle an appreciable interval, filled in front by loose connective tissue, but posteriorly the superficial origin of the protractor hyoidei lies in the space. There is no fusion between this muscle and the protractor hyoidei.

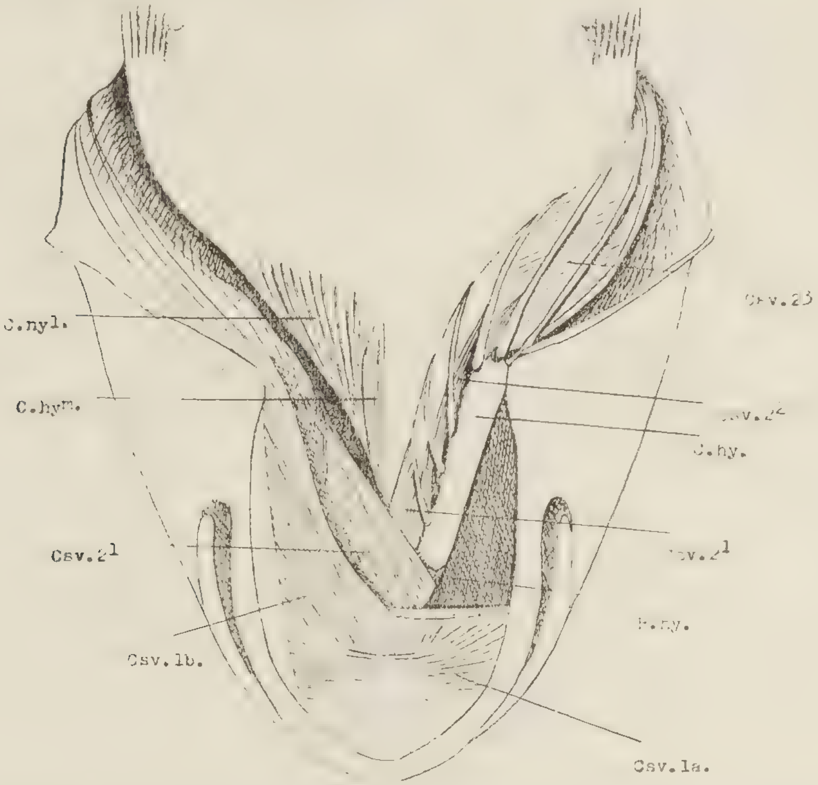


Fig. 22.—*Platycephalus*. Mandibular and hyoid muscles, seen from below, the right side dissected deeper than the left. Csv.1a., M. intermandibularis posterior; Csv.1b., M. protractor hyoidei; C.hy.l. & m., The lateral and medial parts of the M. claviculo-hyoideus; C.hy., The ceratohyoid cartilage; Csv.2, M. hyo-hyoideus; H.hy., The hypohyal cartilage.

Mugil.—In this genus the submentalis is peculiar in being placed dorsally to the protractor hyoidei, immediately beneath the oral mucosa. It is, however, not dorsal to the basihyal (glosso-hyal), which lies in a fold of the oral mucosa which covers it both dorsally and ventrally, so that it projects, as in many other fishes, forward on the floor of the mouth. The submentalis muscle lies beneath the mucosa on which this projecting glosso-hyal lies, with the five dorsal tendons of the protractor hyoidei between them. The muscle arises from a relatively short line along the inner surface of one dentary just below the reflection of the mucosa therefrom. The line commences at the symphysis. All the fibres are quite continuous across the mid-line and are inserted along a precisely similar line of the other dentary.

Amia.—The intermandibularis in this form presents two parts: (*a*) The submentalis (intermandibularis of Allis) which is essentially similar to the submentalis of *Anguilla*. (*b*) The intermandibularis posterior (genio-hyoideus inferior of Allis). This arises on each side from the dentary bone along a line resembling essentially that of the origin of the muscle in *Platycephalus*. The whole of the fibres of both sides reach a median ventral raphe, having a direction slightly caudad to reach their median insertion. There is no attachment of this muscle to the hyoid arch, and, moreover, though inserted into a median raphe common to it and the genio-hyoideus superior (protractor hyoidei of this work), the fibres of the two muscles are at a marked angle to one another and there is fusion of the two muscles.

Anguilla (Fig. 24).—The submentalis in this form is a very small bundle of short muscle fibres which arise from one dentary just beside the symphysis and are inserted into a similar position on the other.

Polypterus.—The intermandibularis posterior is essentially similar to that of *Amia.*

Scomber.—The muscle here is similar to that of *Mugil,* but more extensive, as though it represented that of both *Platycephalus* and *Anguilla* or both anterior and posterior parts of that of *Amia,* but here the two parts are quite continuous and with the posterior rather more reduced than the anterior. It would appear from the description of Allis that the muscle is placed nearly as deeply as is that of *Mugil* (Allis, 1903).

Lepidosteus.—In this form the intermandibularis posterior is an extensive muscle which takes origin from the mandibular ramus along a line which extends from just in front of the joint almost to the symphysis. This line of origin is just beneath the skin. The posterior fibres have a direction caudad and mediad, the fibres in the middle of the antero-posterior length of the muscle pass directly mediad, and those in front of this point incline more and more sharply cephalad. I have been unable, in the small specimens at my disposal, to find any division of the muscle into partes anterior and posterior.

THE PROTRACTOR HYOIDEI.

This muscle was described by Allis under the name of genio-hyoideus superior in *Amia* and genio-hyoideus inferior and superior and hyo-hyoideus superficialis in *Scomber* (1903, 1919), and his first designation for the muscle has been accepted by Herrick (1899) and Norris (1925). Edgeworth (1911) pointed out that the muscle is certainly not the homologue of the genio-hyoideus of higher vertebrates, and to avoid confusion with that muscle he designated this the hyomaxillaris.

Apparently the most extensive study of this muscle yet published is that of Holmqvist (1910, 1911). He bestowed the very apt designation protractor hyoidei upon the muscle. Since this designation has received greater recognition than that of Edgeworth it has been decided to adopt it here. Edgeworth in his later work (1928) rather adds to the confusion by using the designation interhyoideus for the muscle, though he states, " the protractor hyoidei of many teleostei is a compound muscle, being an intermandibularis posterior plus interhyoideus ". If this be so the muscle, in these " many " instances, is not completely homologous with the interhyoideus of the Elasmobranchs, and to that extent the adoption of the name here would introduce confusion.*

The protractor hyoidei is an elongated, flat to oval muscle which arises from the ventral, or, in laterally compressed fishes, lateral, surface of the ceratohyoid anterior to the branchiostegal rays, and passes cephalad and mediad to be inserted into the mandible of its own side just to one side of the symphysis. There is some variation in the muscle in different fishes. The two muscles most commonly fuse anteriorly one with the other along their contiguous mesial margins, and here, as in *Scomber*, there may develop a median, massive, crowding together of muscle fasciculi, giving rise to the appearance of a separate component of the muscle. The insertion onto the ramus of the lower jaw may be placed entirely ventral, entirely dorsal, or partly ventral and partly dorsal to the submentalis muscle. Again, the insertion may be entirely onto the lower jaw or in part into the tough fibrous tissue of the side of the floor of the mouth close to the jaw bones.

In the siluroides *Tandanus* and *Cnidoglanis* (Fig. 23) the condition of the protractor hyoidei is of particular interest. A submentalis similar to that of *Anguilla* is present and is relatively massive. Behind this there is a muscle which resembles an intermandibularis posterior. This arises from the ramus of the jaw on each side of the submentalis and joins its fellow of the other side behind that muscle. There is no intermingling of the fibres of these two muscles. The second muscle is the pars superficialis of the protractor hyoidei. It is a flat sheet of muscle fibres and is continued back, close to the ramus of the jaw, to be inserted onto the upper end of the ventral surface of the ceratohyal close to the lateral edge of that surface, and just lateral to the attachment of the last five branchiostegal rays. The muscle is relatively broad in front and tapers to a point at its most posterior point of insertion. This superficial portion of the protractor hyoidei completely covers the ventral surface of the deeper portion. The deeper portion of the muscle is divided, incompletely, into medial and lateral parts. The pars medialis has a fleshy and tendinous origin from the ventro-lateral surface of the ceratohyal along a line which commences at the point of attachment of the fifth branchiostegal ray, passes forward along the medial margin of the bone to the third ray, and then crosses to the outer margin. The muscle rapidly swells into a considerable bulk and passes cephalad and slightly mediad to be inserted onto the inner surface of the ramus of the lower jaw along a line at the edge between its inferior and medial surfaces for a short distance on one side of the symphysis. This muscle is not fused with its antimere. The pars lateralis is a smaller muscle than the pars medialis but has a more extensive origin from the ceratohyal. This tendinous and fleshy origin covers all the surface of the bone between the origins of the partes superficialis and medialis. The muscle passes forward between the pars medialis and the ramus of the jaw to be inserted into the tough fibrous investment which covers the mandibular periosteum. The point of insertion is just behind the posterior end of the line of insertion of the pars medialis and ventral to the point of issue of the terminal branch of the mandibular ramus of the Vth nerve from the dentary bone.

---

* Edgeworth also appears to have been confused by Allis's terminology, and thereby has added to the confusion Allis (1903) described in *Scomber* an intermandibularis, a geniohyoideus inferior and superior, and hyohyoideus superior and inferior. In a later contribution (1919) Allis says that portion of his geniohyoideus superior constitutes a hyohyoideus superficialis. Now his geniohyoideus inferior in *Scomber* is very certainly not homologous with the intermandibularis posterior of *Amia*, which also he designated geniohyoideus inferior ; it is only a peculiarly developed portion of the geniohyoideus superior. This, apparently, Edgeworth failed to recognize, and, perhaps also misled by the rather peculiar conditions in the Siluridae which he studied in this connection, he regarded Allis's geniohyoideus as synonymous with his interhyoideus and the protractor hyoidei of Holmqvist. Actually the three muscle portions which, in the two contributions, Allis designates geniohyoideus inferior, geniohyoideus superior, and hyohyoideus superficialis, together form the muscle which Edgeworth names interhyoideus and which in this work is termed the protractor hyoidei. The M.hyo-hyoideus superficialis has no real identity, it is but a variant of the M.genio-hyoideus or of the inferior portion of the M.hyo-hyoideus.

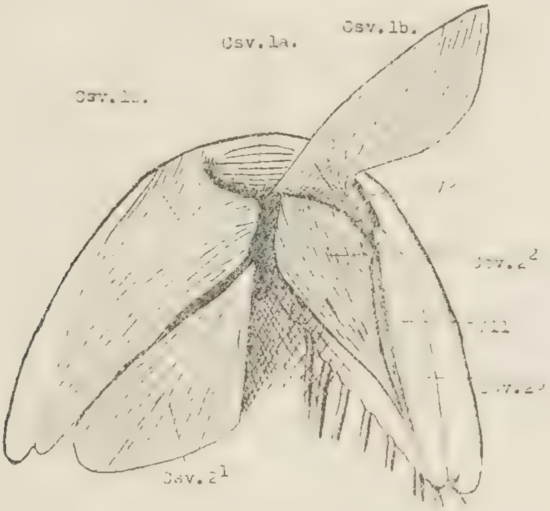


Fig. 23.—*Tandanus.* Mandibular and hyoid muscles, seen from below, the left side dissected deeper than the right. Csv.1a., The M. submentalis; Csv.1b., The M. protractor hyoidei, pars superficialis; Csv.2^1, The M. hyo-hyoideus; Csv.2^2 & 2^3, The medial and lateral parts of the M. protractor hyoidei.

The last two parts are very intimately fused and are inseparable at and near their insertion, but in their anterior two-thirds they separate completely leaving two clean surfaces of contact. There is no fusion between these deeper portions of the muscle and the pars superficialis.

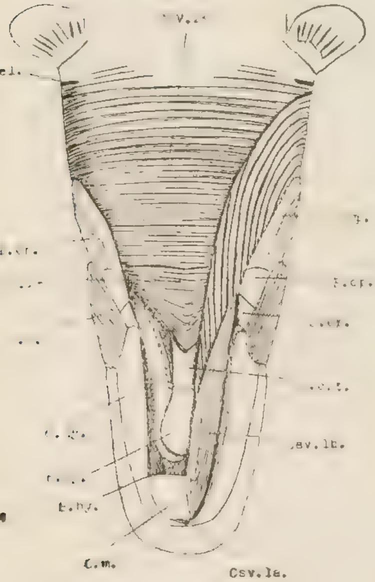
Innervation.—The Vth nerve gives off a brush of fibres as soon as it issues from its foramen, the main trunk continuing forward against the inner surface of the jaw. The brush of fibres are, all but one, distributed over and terminate on the deep surface of the pars superficialis, but confined to the anterior two-thirds of the muscle. The one exception, the largest of the series, turns ventrad and mediad and perforates the anterior tip of the pars lateralis. It was traced caudad between the partes medialis and lateralis and was ultimately lost among the fine tendons of origin of the two parts. No branches were observed to leave this nerve. It is assumed that it is the communicating branch from the VIIth nerve described by Herrick in *Gadus* (1899, p. 157) and in *Amia* by Allis.

In view of the possibility of the exceptional twig being a communicating branch from the VIIth nerve, it is not possible to be quite definite on this question in so far as the pars superficialis is concerned. It is probably innervated by the Vth, but there may also be an innervation by the VIIth. Edgeworth (1928, p. 62) states that in *Silurus* and *Amiurus* this muscle, which he designates intermandibularis posterior, is innervated by the Vth.

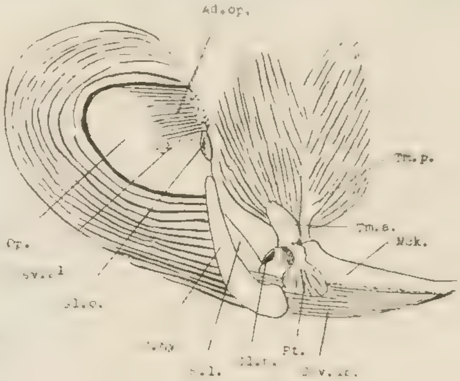
The partes medialis and lateralis are innervated by twigs from the hyomandibular branch of the VIIth nerve which come forward beneath the branchiostegal rays.

This is in accord with Edgeworth's statements in connection with the two siluroids he discusses. He designates these two portions of the muscle the interhyoideus, but says of the muscle that it arises from the cerato- and hypohyal or cerato- and epihyal and " passes inwards and forwards to a median aponeurosis separating it from its fellow, in *Silurus* also by a tendon to the hypohyalia of the same and opposite sides ". It seems possible that this failure to find the insertion onto the ramus of the lower jaw was due to the immaturity of the specimens he studied ; there is also, possibly, some confusion with the hyohoideus, for it seems highly improbable that those two siluroids should have differed so much in the insertion of the protractor hyoidei from the two species I have studied.

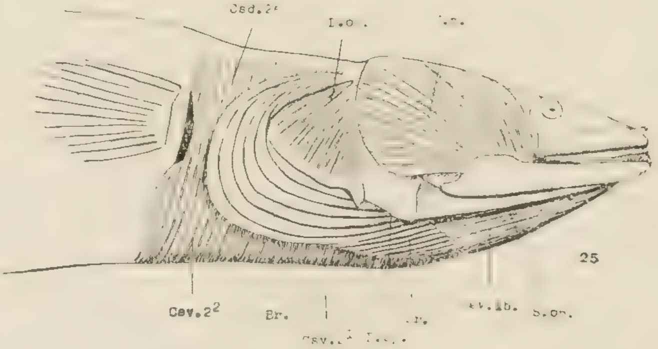
In *Anguilla* (Figs. 24, 25) the protractor hyoidei is an elongated, flattened, muscle which arises in front, from the inferior edge of the dentary to one side of the symphysis by a short rounded tendinous and fleshy origin and passes backward close against the ramus of the jaw to be inserted into the lateral edge of the ceratohyal a short distance behind its joint with the hypohyal, and in front of where the first two or three branchiostegal rays are articulated to it. The muscle



24



26



25

Fig. 24.—*Anguilla*. Mandibular and hyoid muscles. B.hy., Basihyal cartilage ; C.hy., Ceratohyal cartilage ; Csv.1a., The M. submentalis ; Csv.1b., M. protractor hyoidei ; Csv.2^1 & 2^2, The M. hyo-hyoideus ; D.op., The M. dilator operculi ; G.cl., Gill cleft ; H.hy., The hypo-hyal cartilage ; O.m., Oral mucosa ; Op., Operculum ; P.op., Preoperculum ; S-c.t., The sternoclavicular ligament ; S.op., Suboperculum ; T.m., M. temporo-massetericus.

Fig. 25.—*Anguilla*. Lateral view of the same muscles as Fig. 24. Br., The branchiostegal rays.

Fig. 26.—*Anguilla*. The left mandible and ceratohyal cartilage with its branchiostegal rays, with some attached muscles, seen from the medial aspect. Ad.op., The M. adductor operculi ; Gl.m. & Gl.o., The articular surfaces of the mandible and of the operculum ; Csv.2^1, The area of origin of the anterior portion of the M. hyo-hyoideus ; Pt., The tendon of the M. pterygoideus ; Tm.a. & p., Anterior and posterior parts of the M. temporo-massetericus ; S.l., The subopercular ligament.

is quite definitely superficial to the plane of the branchiostegal rays. The muscles of opposite sides are not fused at any point.

Innervation.—Here again the presence of a ramus communicans from the hyomandibular trunk of the VIIth nerve introduces a doubt. Three small twigs from the mandibular trunk of the Vth were observed to terminate on the ventral, superficial, surface of the anterior portion of the muscle. These twigs leave the terminal branch of the trunk just after it emerges from its foramen in the dentary. The terminal nerve continues forward against the inner surface of the dentary, gives off a tiny twig to the submentalis and then breaks up into a brush of sensory twigs behind and to one side of the symphysis.

The ramus communicans from the hyomandibular VII passes forward beneath the opercular bones and the branchiostegal rays, then reaches the lateral edge of the protractor hyoidei and runs forward to the dentary foramen between the muscle and the ramus of the jaw; it joins the fifth just after that emerges from the bone.

Platycephalus (Fig. 22).—The protractor hyoidei of this form arises from the inner surface of the dentary by the intermediary of a strong, but thin, fascial sheet which lies dorsal to the intermandibularis posterior muscle. The two protractor hyoidei muscles are intimately fused at the mid-line along the anterior half of their length. The muscle fibres arise from the fascial sheet just under cover of the posterior margin of the submentalis, and all the area in front of this line between the two jaws and in the plane of the muscle is occupied by the fascial sheet, which, most strongly attached on either side of the symphysis, is also bound to the rami of the jaws on each side as far back as it extends. Behind the posterior margin of the submentalis the protractor hyoidei has a short line of fleshy origin from the dentary, and this line extends just a short distance anterior to the posterior margin of the intermandibularis posterior and superficial to that muscle. The most careful dissection of a number of muscles has failed to discover any trace of division into parts, as in the siluroids, or any fusion of this muscle with the intermandibularis posterior.

Besides the origins just stated, the deeper fibres along the medial margin of both muscles arise from a fascial ribbon which in turn is attached to the lateral edge of the glossohyal.

The muscle passes caudad and slightly laterad, tapering somewhat, to a fleshy and tendinous insertion on the posterior one-third of the ventral surface of the ceratohyal.

Innervation.—The related nerves in this genus are essentially as in *Anguilla*, but in addition there are twigs from the nerve to the hyo-hyoideus which run forward and terminate on the ventral surface of the posterior end of the protractor hyoidei.

Mugil.—The two hyoid protractors are very intimately fused for the greater part of their length. They arise on each side of the symphysis by a fleshy origin ventral to the submentalis and by a tendinous origin dorsal to that muscle. The muscles separate anteriorly in their deeper, dorsal portion so that two fine pencils of fibres pass forward above the submentalis and end in the fine, thread-like tendons.

The anterior two-thirds of the muscles are fused along the mid-line, the posterior thirds diverge to be inserted into the cerato- and hypohyals.

The innervation is as in *Platycephalus.*

The protractor hyoidei in *Girella* is so essentially similar in all respects to that of *Mugil* that it calls for no further comment.

Scomber.—Although Allis (1903) describes this muscle in two parts, superior and inferior, there is no doubt that his pars inferior is but a specialized grouping of the fused medial fibres of the muscle. Having thus cleared the ground, it may be stated that *Scomber* differs from *Mugil* and *Girella* only in that the tendinous and fleshy insertions are, as it were, reversed in their relation to the submentalis.

An examination of a number of other forms enables me to say with some confidence that the anatomy of the protractor hyoidei as above described for *Platycephalus, Mugil, Girella* and *Scomber* is characteristic of the Acanthopterygii.

Amia.—The protractor hyoidei here is a quite simple muscle resembling that of *Platycephalus*, but without the short, more superficial, insertion ventral to the posterior margin of the intermandibularis posterior.

Innervation.—It seems only reasonable to believe that the anterior portion of the muscle is innervated mainly, if not entirely, by the mandibular division of the Vth nerve (Allis, 1898, pp. 613, 614). Herrick (1899, p. 159) says that in *Amia* " the genio-hyoideus (protractor hyoidei and intermandibularis posterior of this work) and intermandibularis (submentalis of this work) are clearly supplied from the V ", but on a previous page (p. 157) he remarks that Vetter says of the protractor hyoideus of *Esox* that it is innervated largely by extension of the ramus hyoideus. After stating that this does not hold for *Menidia*, he continues: " . . . this is, however, true in *Gadus*. Or at any rate the r. hyoideus runs forward from the branchiostegal membrane in this species to anastomose with the nerve for the genio-hyoideus within the substance of that muscle. The figure and description by Allis indicate a similar condition in *Amia*."

These statements are somewhat contradictory, but from the evidence before us it would seem safe to conclude that the posterior end of the muscle is, as in many modern Teleosts, probably innervated by the Vth nerve.

Lepidosteus.—The elongation of the rami of the jaws has been accompanied by changes in the related muscles. The protractor hyoidei is quite continuous medially with the hyo-hyoideus and here the fibres arise from a median raphe. The origin from the ramus of the jaw is, however, preserved by the lateral fibres of the muscle. These arise from the inner surface of the ramus at about the middle of its length. The muscle lies dorsal to the extensive intermandibularis posterior muscle.

Innervation.—This is by an anastomosis between branches from the ramus mandibularis V and ramus hyoideus VII (Norris, 1925, p. 364).

Polypterus.—Here, as in *Amia*, Allis designates the intermandibularis posterior "genio-hyoideus inferior". Having made the necessary correction, it may be stated that the protractor hyoidei in *Polypterus* is essentially similar to that of other bony fishes. For the greater part of its length its medial fibres arise from a median aponeurosis as do those of *Lepidosteus*, this aponeurosis taking the place of the fusion along the mid-line so commonly seen in the modern Teleosts. Posteriorly the muscle is quite continuous with the medial fibres of the hyo-hyoideus as is that of *Lepidosteus*.

Innervation.—Allis (1919, p. 299) is quite emphatic that there is no anastomosis between the contiguous branches of V and VII which may be traced onto this muscle, and that the whole of it is innervated by the Vth only.

Edgeworth (1928) draws what appears to be an arbitrary and unnecessary distinction between those muscles which are completely continuous medially and posteriorly with the hyo-hyoideus and those which are not. Thus the two muscles in *Lepidosteus* are described together as the constrictor hyoideus ventralis, whilst the almost equally fused muscles in *Polypterus* are treated as separate muscles. He draws the same distinction between the homologous muscles in *Polyodon* and *Acipenser*.

Before reviewing these muscles brief reference may be made to the forms described by Holmqvist (1911).

The eel-like *Gymnarchus* is remarkably similar to *Anguilla*. It is probable that in this form, as in the Eels, there is a small submentalis. *Albula* presents an arrangement of the muscles which may well be regarded as an intermediate condition between those of the Eels and the normal Acanthopterygii. *Esox* is very similar to *Platycephalus*, the fibres of the intermandibularis having, however, a diagonal direction in place of one directly transverse. *Salmo*, *Osteoglossum*, *Abramis*, *Raniceps*, *Perca*, *Zoarces* and *Callionymus* are but modifications of the normal acanthopterygian type. One questions whether a small submentalis is not present in *Barbus*. In nearly all of these forms the identification which Holmqvist makes of the intermandibularis posterior is quite arbitrary. *Siluris glanis* is essentially similar to *Tandanus* and *Cnidoglanis*.

REVIEW OF THE SUBMENTALIS, INTERMANDIBULARIS POSTERIOR AND PROTRACTOR HYOIDEI.

Holmqvist found, as I have found, that the submentalis, intermandibularis posterior, and anterior portion of the protractor hyoidei in the bony fishes generally are innervated by the Vth nerve, whilst the posterior portion of the last was innervated by the VIIth nerve. Quoting direct from Allis, "Holmqvist (1911) says that the intermandibularis and protractor hyoidei of all the bony fishes are derived, respectively, from the mandibular and hyal portions of the primitive musculus constrictor ventralis. The primitive condition of the intermandibularis (submentalis plus intermandibularis posterior) is said to have been that of a muscle extending transversely from one ramus of the mandible to the other, and this condition is said to be actually found in the Selachii, in *Lepidosteus* and Teleostei, and in *Amia*, the muscle is said to have undergone a vertical cleavage into two parts, one of which is called the intermandibularis I (submentalis) and the other the intermandibularis II (intermandibularis posterior) . . . The protractor hyoidei is said to be . . . derived from that deeper layer of the constrictor ventralis of the Selachii that has its insertion on the cerato-hyal." This, of course, is the interhyoideus of the earlier pages of this work.*

The development of these muscles in the Ganoids and in *Caranx* has been studied by Edgeworth (1928) and his observations appear to confirm the conclusions of Holmqvist.

With these conclusions I am in almost entire accord, but would particularize a little further.

The observations of Edgeworth on *Caranx trachurus* clearly prove that which may well have been anticipated from the innervation and anatomical relations of the muscles. The protractor hyoidei is in most bony fishes, if not in all, a composite muscle derived from the posterior portion of the Csv.1 and from the interhyoideus.

The submentalis is derived from the anterior portion of the Csv.1 and is completely homologous throughout the bony fishes.

The intermandibularis posterior is a derivative of the posterior portion of the Csv.1. It may maintain its identity, as in *Polypterus*, *Amia* and, perhaps, *Platycephalus*, or it may lose its identity in part, as in the Siluridae, or completely, as in the majority of Teleostoi, by fusion with the anterior end of the protractor hyoidei.

The constant innervation of the anterior end of the protractor hyoidei by the Vth nerve in those forms in which the intermandibularis posterior maintains its identity leads us to believe that this anterior portion of the protractor is derived from a portion of the Csv.1 posterior to that from which the intermandibularis posterior was derived. It is not improbable that this portion of the mandibular muscle plate had become attached to that of the hyoid segment prior to the earliest stages studied by Edgeworth. It is noteworthy that in *Amia* and in *Lepidosteus* the two muscle plates are continuous at the earliest stages he describes, and that his earliest stages of *Polypterus* are a good deal more advanced than are those stages of *Caranx trachurus* in which he demonstrates the fusion of the intermandibularis posterior and the anterior end of the protractor.

The submentalis muscle fibres are quite continuous across the mid-line from one ramus of the jaw to the other; the fibres of the intermandibularis posterior are, with the exception of a few along its posterior margin, inserted into a median tendinous raphe. This leads to the suggestion that the muscle in *Lepidosteus* is, as already indicated above, an intermandibularis posterior, and that no submentalis has been developed, and that the intermandibularis posterior only is present in *Polypterus*, as suggested by Edgeworth (1928, p. 60). Contrariwise, the submentalis only is present in the majority of the Teleostei, the intermandibularis posterior having been completely submerged in the protractor hyoidei.

The condition of these muscles in the siluroid fishes raises another question, which, however, we can do little more than raise in the present state of our knowledge of their development. May it be that in these fishes the pars superficialis of the protractor hyoidei is developed from the anterior portion of Csv.2 and posterior portion of Csv.1, whilst the partes medialis and lateralis are derivatives of the interhyoideus, and, if so, does it follow that the protractor hyoidei of the majority of the Teleostei is compounded of these three derivatives?

Remembering that there is always an overlapping of the innervation of Csv.1 and Csv.2 along their contiguous, and inseparable, margins, this seems not improbable.

THE HYO-HYOIDEUS.

Platycephalus (Fig. 22).—(1) Pars anterior (Csv.2^1) arises from the lateral margin of the hypohyal and passes caudad obliquely across the mid-line to be inserted into the median edges of the first and second branchiostegal rays. The muscle is a triangular sheet having a fleshy origin from the hypohyal, and in its course to its insertion that arising on the right side passes ventral to the hypohyal and also ventral to the hyo-hyoideus arising on the left side. The muscle tapers posteriorly and is inserted by a relatively long tendon. (2) Partes abductores branchiostegalium (Csv.2^2) are four little muscles which are placed in the interspaces between the bases of the first five branchiostegal rays. Each arises from the base of the ray in front, from the capsule of its joint with the ceratohyal, and from the ceratohyal close to that capsule, and is inserted onto the antero-medial edge of the ray behind a short distance from its base. (3) Partes adductores branchiostegalium (Csv.2^3) are three narrow, thin sheets of muscle fibres which fill the interspace between the full length of the last four rays. (4) Pars dorsalis is an extensive, thin sheet of muscle fibres which arises from the lateral edge of the last branchiostegal ray, the seventh, and passes dorsad to be inserted into the dorsal margin of the operculum and into the fascia dorsalis under cover of that bone.

---

* Since the above was written I have been able to consult Holmqvist's two papers, but find no need for addition to or emendation of the foregoing quotation and remarks.

Innervation.—This is by the hyoid branch of the VIIth nerve. The nerve reaches the superficial surface of the muscle under cover of the operculum, and its numerous twigs course mediad and cephalad on the surface of the muscle, but they dip beneath, i.e. dorsal to, the branchiostegal rays as they pass them.

It appears that the pars anterior, acting in conjunction with the branchiostegal abductors, acts to open out the whole branchiostegal membrane, whilst the remainder of the muscle has an opposite action.

The hyo-hyoideus of *Platycephalus* has been selected for detailed description because it is a remarkably complete muscle. This is an exceedingly variable muscle, and in the numerous fishes which have been examined the pars anterior alone is constantly present. The pars dorsalis is, in my experience, the portion of the muscle that is most commonly absent. In some forms either the abductors or the adductors are found definitely deep to the branchiostegal rays, so that in my earlier dissection notes I described them as branchiostegalis profundus and superficialis, but later, discovering that there was no constancy as to which was deep and which superficial, the designations were abandoned in favour of those used above.

In the Apodes the hyo-hyoideus is quite peculiar and very unlike the muscle in the rest of the Teleostei.

Anguilla (Figs. 24, 25).—Pars anterior is a relatively broad ribbon of muscle which arises from the postero-lateral edge of the skull below the sulcus for the head of the hyomandibular and from the deep surface of the operculum just below its joint with the hyomandibular. This line of origin is much shorter than the width of the muscle ventrally, for as the fibres pass toward the ventrum of the fish they diverge, extending cephalad well forward of their origin. The most posterior fibres pass directly ventrad.

Pars posterior is a very broad sheet of muscle fibres which, like the anterior part, lies in contact with the mucosa of the side wall of the mouth and atrio-pharynx. It arises from the fascia dorsalis along a line which commences in front, immediately behind the postero-lateral and dorsal corner of the skull, above the articulation of the operculum to the hyomandibular, and extends back to just above the root of the pectoral fin. From this origin the fibres pass directly ventrad to the mid-line ventrally. A narrow, yet not linear, tendinous interruption intervenes between the dorsal third, and ventral two-thirds of the sheet for a short distance at the level of the dorsal margin of the fin. This interruption commences just in front of, and dorsal to, the gill slit and extends forward a little past the middle of the antero-posterior length of the sheet.

Both parts of this muscle are quite uninterruptedly continuous, across the mid-line ventrally, with the muscle of the other side. There is no trace of any attachment of either part to any element of hyoid or branchial arches.

Both muscles lie deep to the operculum and to the branchiostegal rays. These may be quite readily dissected free from the underlying muscle and that in turn from the structures deep to it. The fibres of the two muscle parts are parallel at their contiguous margins, but it is always possible to separate them along this line, which lies immediately behind the last fasciculus arising from the deep surface of the operculum, between it and the most anterior fasciculus arising from the fascia dorsalis; separation at no other point can be effected without splitting fasciculi.

Innervation.—This is by twigs from the hyoid branch of the VIIth nerve, which are distributed over the surface of the muscle beneath the operculum and branchiostegal rays.

There is little room for doubt that the hyo-hyoideus of the bony fishes is a derivative of the hyoid constrictor sheet of the Elasmobranchs, the Csd.2 and Csv.2.

We have already noted that the anatomy of the protractor hyoidei in the Siluridae suggests the possibility that the most anterior of the Csv.2 fibres enter into the formation of the superficial portion of that muscle.

Later, it will be necessary to discuss the possibility that other Teleost muscles are derived from the dorsal part of the Csd.2.

THE HYOID MUSCLES OTHER THAN THE CONSTRICTORS.

There are four of these muscles, the adductor arcus palatini, the adductor hyomandibulae, the adductor operculi and levator operculi.

The Adductor Arcus Palatini and the Adductor Hyomandibulae.

Platycephalus.—In this fish, as in *Scomber* (*fide* Allis) these two muscles are quite interruptedly continuous. They arise from the lateral edge of the synpterygoid (parasphenoid). The origin extends from a little in front of the middle of the antero-posterior diameter of the orbit back to the myodomial boundary and then dorsad half-way round that boundary, and is also carried back along the same bone to the prootic. The insertion is onto the ventral surface of the palatal arch along a line which commences on the outer edge of the palatine just where that sutures with the maxilla, runs back along the palatine and then along the suture between the palatine and quadrate, next along the mesial, free margin of the metapterygoid, to terminate at the suture between this last and the prootic bone.

The muscle is thickest near its posterior end and becomes quite a thin sheet anteriorly.

Innervation.—The posterior margin of the muscle lies ventral to the fascialis foramen. The hyomandibular trunk of the VIIth nerve passes laterad and slightly caudad from the foramen, and appears behind the middle of the posterior edge of the muscle. Just before it comes into view, the motor nerve to these two muscles is given off. The nerve enters the dorsal surface of the muscle close to the posterior margin and runs forward in the muscle nearer the ventral than the dorsal surface and about the middle of its width ; twigs trending both mediad and laterad are given off at intervals along its length.

In no one of the fishes which I have dissected have I been able to find a clean plane of cleavage between a portion of this muscle, which might be regarded as an adductor of the hyomandibular, and a portion which might be regarded as an adductor of the arch of the palate. It is noteworthy that in the more primitive forms there is developed only so much of the muscles as is inserted into the hyomandibular ; the reference here is, of course, to *Amia* and *Polypterus*.

Apparently in *Menidia* the two portions of the muscle are separated, for Herrick (1899, pp. 137, 138) describes separate motor nerves in that fish to the two muscles.

The Adductor Operculi.

Platycephalus.—This is a relatively massive muscle which arises from the inferior surface of the pterotic and opisthotic, the origin covering the whole of those surfaces. The general direction of the fibres is laterad and dorsad, parallel to the surface of origin. The fibres converge somewhat to be inserted onto the inner surface of the operculum immediately behind the articular head. For the most part this insertion is onto the base of a strengthening rib, on the inner surface of the bone, which commences at the head and extends to the postero-dorsal corner.

Innervation.—The motor nerve to this muscle leaves the hyomandibular trunk just after that to the last muscle, and plunges into the muscle after crossing the exposed bare surface of the prootic bone which lies between the anterior margins of this muscle and the posterior margin of the adductor arcus palatini in front.

There is some variation in the site of origin and the manner of insertion of this muscle in different fishes, but none of these is of sufficient importance to call for separate description.

The Levator Operculi.

Platycephalus.—The levator operculi appears in this fish as though it were the dorsal continuation of that portion of the pars dorsalis of the hyo-hyoideus which is inserted into the inner surface of the operculum. It arises from the dorso-lateral edge of the skull behind the operculo-hyomandibular joint, and in this origin is continuous with that portion of the hyo-hyoideus which has a similar origin behind it. It is inserted onto the dorsal edge of the operculum. It lies immediately beneath the skin and upon the adductor operculi, where that passes across the narrow interval between the operculum and the skull.

Innervation.—The motor nerve in this muscle is a twig from that branch of the hyomandibular which Herrick (1899) calls the ramus hyoideus and which is essentially the motor nerve to the superficial hyoid muscles, the hyo-hyoideus and posterior end of the protractor hyoidei.

Throughout the bony fishes the levator operculi is essentially as in *Platycephalus*. Its origin appears to be constantly from the postero-lateral corner of the skull. Commonly this origin is more restricted than the insertion, so that the fibres diverge fan-like from the origin. Again it is common for the insertion to extend over more or less of the superficial surface of the operculum. In some fishes the muscle is more or less fused with the adductor operculi, e.g. *Amia* and *Anguilla* (Figs. 25, 26).

Review.

Whilst their development places it beyond doubt that these four muscles, together with the hyo-hyoideus and posterior end of the protractor hyoidei, are all hyoid muscles, their innervation by two widely separated branches of the facial nerve separates them into two groups, superficial and deep.

Of the four which we now discuss, three belong to the latter group and one only to the former ; this last is the levator operculi.

This muscle had been homologized in the past with that which it seems so obviously to represent in *Platycephalus*, portion of Csd.2. There appears no reason to doubt that this homology is the correct one.

Turning our attention to the Selachii, it will be remembered that in those fishes the dorsal end of the hyoid muscle plate gave rise, deep to the constrictor sheet, to the levator hyomandibulae, and that in the adult this muscle lies behind the spiracle and the hyomandibular branch of the facial nerve, in contact with the deep surface of the Csd.2. The muscle arose from the skull behind and above the auditory capsule and was inserted onto the superior and anterior surface of the hyomandibular cartilage.

In those fishes in which the adductor hyomandibularis is separated from the adductor arcus palatini, or in which that muscle is not developed, *Amia* and *Polypterus*, this hyoid adductor preserves all the relations of the hyoid levator of the Selachii. It is, moreover, developed from the dorsal portion of the hyoid muscle plate deep to the primordium of the hyo-hyoideus.

Since the adductor arcus palatini and the adductor operculi are also developed from the same primordium, and in some fish never become separated from the hyomandibular adductor, it were unreasonable to refuse to regard all three muscles as being derivatives of the elasmobranch hyoid levator.

MANDIBULAR MUSCLES OTHER THAN THE VENTRAL CONSTRICTORS.

In this group there are the following muscles : the levator arcus palatini, the dilator operculi and the mandibular adductor muscles.

The Levator Arcus Palatini.

Platycephalus (Fig. 27).—The muscle arises from the side wall of the skull behind the orbit and from a cranio-palatal fascial partition between it and the adductor arcus palatini mesial to it. This area of origin extends from the posterior boundary of the orbit caudad to the inferior margin of the dilator fossa above and the suture-line between the prootic and os transversum below. These two boundaries meet at the anterior margin of the hyomandibular facet. The general direction of the fibres is caudad and laterad. The deeper and more anterior fibres are inserted into the flange which stands out from the outer surface of the metapterygoid and into that bone itself above the flange. The more posterior and superficial fibres pass superficial to the postero-medial corner of the origin of the pterygoideus to be inserted into the suture-line between the hyomandibular and the preoperculum.

The postero-medial corner of the origin of the pterygoideus referred to runs upward and backward deep to the insertion of the deeper fibres of the levator arcus palatini, lying in the angle between the flange and the main part of the os transversum.

Innervation.—This is by a branch from the mandibular ramus of the Vth nerve which leaves the main nerve under cover of the muscle and curves round its anterior margin, and then passes caudad over its surface and ends in the dilator operculi. Several twigs are given off to the muscle as it passes over it.

Paradicichthys.—It was not intended to attempt a description of the cranial muscles, nor, indeed, would this have been possible in a satisfactory measure from a single specimen. As the preparation of the skull progressed, however, the arrangement of the muscles was noted, and certain peculiarities of the levator arcus palatini which were observed are deemed worthy of mention. (See p. 105 for description of the skull.)

The muscle is clearly divisible into three divisions. Of these, the first may be termed the abductor hyomandibularis. This is a digastric muscle; the upper belly arises from the outer portion of the floor of the dilatator fossa and the back of the upper post-ocular scute, its fibres gathering into a broad, short tendon which passes down and back through that foramen described as formed between the shelf-like process on the upper outer face of the body of the hyomandibula and the outer corner of the post-orbital lamina of the sphenotic. The foramen in question is to a large extent closed by a strong membrane. The fibres of the lower belly of the muscle are attached to the outer face of the hyomandibula below the "shelf", and above and in front of the ridge which crosses the body diagonally to the antero-inferior corner of the bone. These fibres arise from the tendon as it spreads out immediately it passes through the foramen.

The second division of the muscle may be termed the abductor arcus palatini. This arises as a strong cord-like tendon from the back of the lower post-ocular scute and from the outer corner of the post-orbital lamina of the sphenotic; the tendon passes directly downward and through the narrow foramen between the two laminae of the hyomandibula and os transversum, then opens out and gives origin to muscle fibres which are attached to the inner surface of the epipterygoid over the area already described.

The third division of the muscle, which may be designated the levator arcus palatini, sensu stricto, is essentially similar to the anterior portion of the muscle in *Scomber*, as described by Allis (1903).

It may be stated that the three divisions of the levator arcus palatini just described can be recognized in the great majority of fish, but it is only in a few that the divisions are as distinctly separable as in the present case.

The above may be accepted as a description of the levator arcus palatini as it is found in the majority of the modern Teleosts.

In the two Siluroid fish I have been able to dissect, the muscle is much reduced. It is a small flat muscle which arises from the dorso-lateral edge of the skull in front of the posterior end of the hyomandibular joint and passes ventrad to be inserted into the dorsal margin of the hyomandibular just below the joint.

Lepidosteus.—In this fish the hyomandibular portion of the muscle is differentiated from the more anterior portion. Allis recognizes levator arcus palatini and retractor hyomandibulae, as well as dilator operculi and the specialized slip of the latter which he terms muscularis spiracularis.

PROTRACTOR MAXILLAE OF THE SILURIDAE AND LEVATOR MAXILLAE SUPERIORIS PART 4 OF AMIA.

The protractor maxillae of the two siluroid fish *Tandanus* and *Cnidoglanis* is a relatively thick muscle which arises from the side of the skull above the anterior attachments of the palatal arch, and passes caudad and laterad to be inserted onto the posterior end of the maxilla, the insertion enswathing the posterior end of the bone on all but its deep surface.

Innervation.—This is by a branch from the Vth nerve which leaves the anterior and inferior surface of the mandibular ramus deep within the orbit.

The little muscle which Allis (1897) described as the fourth part of the levator maxillae superioris in *Amia* appears to be strictly comparable with this protractor muscle.

THE DILATOR OPERCULI.

Platycephalus.—The muscle arises from the dilator fossa and passes caudad and laterad deep to the dorsal tip of the preoperculum and is inserted into the superficial surface of the operculum just beyond the capsule of its joint with the hyomandibular.

Innervation.—This is by the terminal twig of the motor nerve from the mandibular ramus of V to the levator operculi, as described above.

In *Tandanus* and *Cnidoglanis* the dilator operculi is a relatively massive muscle which arises deep to the levator arcus palatini from the side wall of the skull above the anterior end of the long hyomandibular articulation.

EXCEPTIONAL MUSCLES OF THE MANDIBULAR SEGMENT.

In various of the more or less aberrant Teleosts there are found muscles which are without close parallels in the more normal fishes. Their innervation and anterior situation indicate that these are derivatives of the mandibular muscle plate, and probably from the dorsal portion. They are, therefore, probably derived from that portion of the mandibular muscle primordium from which are derived the last two muscles. For this reason they are briefly referred to here.

(1) *The Retractor labii superioris of Drepane.*—This is a fine thread-like strand of muscle fibres which arises from the medial surface of the preorbital bone and passes directly forward along the dorsal edge of the ascending process of the premaxillary labial bone to be inserted into that edge close to the junction of the process and the body of the bone.

Innervation.—This is by a very delicate twig from the mandibular trunk of the Vth nerve which leaves the main nerve deep within the orbit and runs forward below the ophthalmic ramus of the nerve.

(2) *The erector muscles of the barblets in the siluroid fishes.*—In the two which I have dissected the muscle to the median barblet arises from the dense connective tissue over the side of the mesethmoid in front of the prefrontal and slightly behind the base of the barblet. That of the labial barblet arises from the periosteum of the maxillary labial bone. Herrick (1901) writes of a slip of the adductor mandibulae which functions as the adductor of the maxillary barblet in *Ameiurus.* There is no such slip present in either of the fishes I have studied.

THE MANDIBULAR ADDUCTOR MUSCLES.

Before describing these muscles it is advisable to present an explanation of the nomenclature adopted. To this end it is necessary to summarize briefly again the findings relative to these muscles in the lower tetrapods.

Reviewing the relation of the components of the masticatory complex and commencing with the muscles of the reptiles, we have:

(1) A superficial sheet of fasciculi, the Retractor anguli oris, which is superficial to all three branches of the Vth nerve;

(2) An almost superficial mass of fibres, the Temporalis, which also is superficial to all the branches of the Vth nerve;

(3) A deeper layer, the Massetericus, which may or may not be inseparably fused with the last and, like it, lies superficial to the branches of the Vth nerve. The origin of this and of the last muscle is from the skull dorsal to and behind the foramen of the Vth nerve;

(4) A deep mass of fibres, the Pterygoideus externus, which may or may not appear in part superficially at their origin, which pass to their insertion anterior to the foramen of the Vth nerve, are crossed superficially by the ramus maxillaris, and are inserted into the lower jaw in front of and/or medial to the ramus mandibularis V just as that enters Meckel's fossa;

(5) A deep mass of fibres, the Pterygoideus medius, which arise from the wall of the skull ventral to, and either in front of and/or behind, the foramen of the Vth nerve. The muscle is crossed superficially by the ramus mandibularis and, it may be, also by the ramus maxillaris; and

(6) Another mass of fibres, the Pterygoideus internus, very deeply placed, which arise from the upper surface of the roof of the palate and from the side wall of the cranium behind the via masticatoria. This lies deep to all the other components and the ramus mandibularis is, of course, superficial to it, with the pterygoideus medius between.

The essential facts are (1) the temporalis and massetericus are superficial to the nerve rami; (2) the pterygoideus externus is crossed between origin and insertion by the R.max. and is either inserted in front of the R.man. or is internal to the nerve at its insertion; (3) the pterygoideus medius and internus lie deep to both rami of the nerve, and for the most part behind them.

In the Amphibians the same relations hold good. The pterygoideus medius is never developed and the pterygoideus internus only in the Coecillians. Here again the relations to the rami mandib. and max. are constant and are just as in the Reptiles.

Turning next to the Dipnoans, it is found that there are but two separate portions of the adductor muscle mass. It is significant that these two portions are separated by the two rami of the Vth nerve. There appears no reason to doubt that the anterior portion may be identified as the pterygoideus externus, whilst the posterior portion must represent either or both the temporalis and masseter.

In an attempt to recognize the forerunners of these muscles amongst the fishes, one may turn to the Holocephali. In these Elasmobranchs there is a small adductor mandibulae which lies entirely behind the rami of the nerve, and anteriorly a massive adductor and a series of smaller ribbon-like muscles which activate the upper lip. These latter all lie deep to the ramus maxillaris. It were little short of unsupported speculation to attempt to homologize the ribbon-like muscles, but the function of the larger adductor muscle and its relation to the two rami of the nerve fully justify its identification as the pterygoideus externus of the Dipnoi and the Tetrapods. The most serious objection to this identification is its origin, in front of the orbit instead of behind it. This, however, will be seen later to be not so serious, as it will be found that other, undoubtedly homologous, muscles are found in bony fishes arising behind or in front of the orbit in different species, and that in the cockatoos the pterygoideus externus arises in front of the orbit.

Comparison of the muscles of the Holocephali with those of *Chiloscyllium* enables one to recognize at once the homologous muscles. The pterygoideus externus is that which lies in front of the two rami of the Vth nerve, and the comparison of the muscles of *Chiloscyllium* with those of the rest of the Plagiostomes leads one to the inevitable conclusion that if the forerunner of the pterygoideus externus is recognizable at all in the Elasmobranchs it can be none other than the muscle which Vetter designated the " Add. β " and Marion, the " Levator labii superioris ".

Apparently the temporalis and the masseter are represented in the complex quadrato-mandibularis of the Elasmobranchs, and it is not improbable that the relatively constant subdivision of that muscle which is described in this work actually foreshadows the subdivision of the muscle into the components found in the Tetrapods.

Turning now to the Bony Fishes, and commencing with *Polypterus*, the mandibular adductors present division into four readily separable parts. Of these, two lie superficially to the rami of the nerve and are inserted onto the mandible superficially to or behind the R.mand. These Allis described as the superficial and deep portions of the adductor mandibulae. It would appear that the superficial portion is the homologue of the temporalis, and that the deeper portion is the homologue of the masseter. There are also two divisions of the adductor muscles lying deep to, and inserted medial to, the rami of the nerve. The more superficial of these was designated the temporalis by Allis. This it cannot well be on the evidence of its relation to the nerves. It appears quite reasonable to identify it as the precursor of the pterygoideus medius, and the other arising further forward as the pterygoideus externus.

In the modern Teleostei the ramus maxillaris of the Vth nerve runs forward dorsally to the origin of all the muscles. There are no muscles lying deep to this ramus, and it fails us as a reference structure.

In *Amia*, however, there are two little muscles arising far forward and crossed superficially by the R.max. and further back the great bulk of the adductor muscles lie deep to the R.mand. Now in this fish the only adductor muscle to be inserted externally to the R.mand. and to lie entirely superficial to the ramus is that which Allis described as the lower portion of the superficial part of the adductor mandibulae. Although Allis stated that the separation of this portion of the muscle was wholly artificial, I find that the cleavage plane occupied by the ramus mandibularis beneath this portion is quite clean and very definite.

If the relation to the ramus mandibularis be a determining factor, then this superficial portion of the adductor mandibulae must be the homologue of the muscles superficial to the ramus in the Tetrapods, that is to say the temporalis and the masseter.

Throughout the rest of the Bony Fishes we find always two main divisions of the adductor muscles ; there is always one portion which is superficial to or arises behind the R.mand. and is inserted onto the mandible lateral to it, and there is the other portion which arises in front of the ramus or deep to it and is inserted onto the mandible medial to it. These vary in their relative and actual size—now one, now the other is the larger.

It is believed that it is correct, or at least reasonable, to regard the former as representing the temporo-masseteric group of the Tetrapoda and the latter as representing the pterygoid group.

In conformity with this belief, and in order to maintain an uninterrupted sequence in the nomenclature, the mandibular adductor muscles of the bony fishes are described in the following pages as temporo-masseteric and pterygoid.

The question arises, however, as to just what is the homology of these two divisions with the adductor muscles in the Elasmobranchs. In these fishes there is by no means such a clear-cut division into two divisions. The homology of the muscle which, in this work, has been designated " M. pterygoideus " throughout the whole of the vertebrata is believed to be sufficiently supported by the available evidence to justify the designation. On the other hand, the quadrato-mandibularis of Elasmobranchs is very generally perforated by the ramus mandibularis of the

Vth nerve, and this suggests that its deeper portion may be homologous with the posterior portion of the pterygoid of the bony fishes and with the Mm. pterygoideus medius and internus of the Amphibians and Reptiles.

This question is returned to in the later sections of the work.

THE TEMPORO-MASSETERIC GROUP OF MUSCLES.

These muscles were described by Vetter as the first and second divisions of the adductor mandibularis, the "A^1" being that which I describe as the pars anterior, and "A^2" the pars posterior. Allis describes the pars anterior, in *Amia*, as the first part of the levator maxillae superioris; the pars posterior he describes as portion of the superficial portion of the adductor mandibulae (A^2). In *Scomber* there is no separate pars anterior, and Allis describes the muscle as the superficial portion of the adductor. In *Polypterus* the pars anterior, particularly well developed, is termed "temporalis" by Allis, whilst the pars posterior he describes as the superficial portion of the adductor.

In discussing *Callorhynchus* (1933) I designated the pars anterior "adductor labii superioris", and the pars posterior the "retractor anguli oris".

The muscle presents a wide range of variability and a number of these variations will be described.

Platycephalus (Fig. 27).—(A) *Pars anterior.* This is a relatively stout three-sided bundle of fibres which lies medial and dorsal to the other adductor components and between them and the levator arcus palatini. The fibres for the most part arise from the superficial deep fascia, but a few arise from a very thin superficial tendon which lies upon the posterior half of the superficial surface of the muscle, and is itself attached to the anterior edge of the subdermal ridge of the preoperculum below the point whereunder the dilator operculi passes. The general direction of the fibres is cephalad, with an inclination ventrad and laterad, to an insertion into a strongly developed tendinous strand in the maxillo-labial fascia. This strand is attached behind to the ascending process of the lower jaw; in front it is attached to the posterior edge of the maxillary labial bone close to the articular head. This ligament is so very constantly present that it is proposed to recognize and establish its identity by the designation mandibulo-labial ligament (ligamentum mandibulo-maxillare posterius of Holmqvist, 1911).

The maxillo-labial fascia is a strong membrane which is attached medially to the lateral edges of the maxilla and palatine bones, posteriorly to the anterior edges of the ectopalatine, inferiorly to the inner surface of the articular and/or posterior end of the dentary below the insertions of the mandibular adductors. In front of this last attachment, the fascia presents a free margin in the fold of the lip at the angle of the mouth and is attached in front of the angle to the internal surface of the full length of the inferior edge of the maxillary labial bone. Between this and the premaxillary labial the fascia is folded with the skin to provide the loose membrane between these two bones which permits of the protrusion of the two labial bones.

This fascia also is of very constant occurrence and in the absence of the mandibulo-labial ligament, which is but a specialized portion of the fascia, provides the retractor ligament of the upper lips and their enclosed bones. The free edge of this fascia in the lips at the angle of the mouth is the ligamentum mandibulo-maxillare anterius of Holmqvist.

(B) *Pars posterior.* This is a very massive muscle which arises from the whole of the lateral surface of the preoperculum, except its subdermal ridge, and from the hyomandibular and the deep surface of the posterior suborbital. The whole of the fibres are inserted into a fan-like tendon which divides the muscle into superficial and deep portions. The fibres arising from the hyomandibular and preoperculum are inserted into the broad, thin posterior edge of this tendon and into its deep surface. Those arising from the subocular bone are inserted onto its superficial surface.

The tendon, contracted to a narrow ribbon, is inserted onto the tip and inner surface of the ascending process of the mandible above Meckel's foramen. Its anterior edge is reflected away from the mandible and is bound to the thickened edge of the maxillo-labial fascia and to the mandibulo-labial ligament.

Anguilla (Figs. 24, 25, 26).—(A) *Pars anterior.*—This arises from (1) a medial dorsal septum from the other side of which its fellow arises, and which commences just behind the orbit and extends back to just beyond the posterior limit of the skull; (2) a triangular membrane which covers, but is not attached to, the anterior end of the trunk muscles immediately behind the skull and slopes backward over the adductor and levator operculi; (3) the whole of one side of the dorsal surface of the skull behind the level orbit. The ventro-lateral surface of the muscle is clad by an expanded tendinous sheet, and it is into this sheet that the muscle fasciculi are inserted.

(B) *Pars posterior.* This arises from (1) a strong narrow band membrane which lies behind and beneath the posterior boundary of the muscle. This band commences above at the triangular membrane behind the pars anterior and passes laterad attached to the posterior edge of the skull, then ventrad and cephalad over the origins of the adductor and levator operculi and the insertion of the dilator operculi, and below that is attached to the posterior edge of the quadrate; (2) the lateral surface of the hyomandibular below the dilator operculi and the contiguous surface of the quadrate. As in the case of the pars anterior, the deep surface of the muscle is clad by an expanded tendinous sheet into which most of the fasciculi are inserted.

The two deep tendons taper as they proceed ventrad, laterad and cephalad towards the ascending process of the lower jaw. Before this is reached they combine to form one broad thick tendon. This is inserted onto the edge of the ascending process of the dentary and inner surface of the bone above, lateral to, and in front of, Meckel's fossa. The tendon is completely covered by the fasciculi of the two parts of the muscle, which are here completely fused. The fusion extends backward for a little less than one-third of the length of the contiguous surfaces.

Mugil (Fig. 28).—In this form the temporo-massetericus is represented by a single muscle in which no division is present. It arises from the inferior edge of the quadrate and a contiguous narrow area low down on the preoperculum. It is a relatively small flat muscle, broader behind, which tapers as it passes forward. Its fasciculi are inserted into a tendon which lies along its dorsal edge and which takes the place of the mandibulo-labial ligament and is inserted into the mandibular labial at about the junction of its middle and outer thirds.

Girella (Fig. 29).—(A) *Pars anterior.* This is a roughly four-sided muscle which arises from the preoperculum behind the orbit. It runs forward, under cover of the orbital scutes, below the orbit and has an insertion into the middle of the length of the maxillary labial by a tendon so short as to give it the appearance, almost, of having a pointed fleshy insertion. The deeper fasciculi are inserted into a tendon on its deep surface, which is bound to the maxillo-labial fascia.

(B) *Pars posterior.* This arises from the lower half of the edge of the subdermal ridge of the preoperculum. The muscle is inserted into the maxillo-labial fascia just behind the free margin of the fascia at the angle of the mouth. This insertion is as broad as the full width of the muscle, and is continued onto the ascending process of the dentary above Meckel's fossa on the one side, and is closely bound to the inferior edge of the pars anterior above it on the other.

Zanclistius.—In this fish, as in *Mugil*, there is but a single muscle. It arises from the anterior edge of the upper half of the vertical limb of the subdermal ridge of the preoperculum and from a very narrow area of the bone in front of the edge. It passes nearly horizontally forward to be inserted into the free edge of the maxillo-labial fascia and into the proximal end of the mandibulo-labial ligament.

Drepane.—Here also the temporo-massetericus muscle is not divided. It is an extensive sheet, of moderate thickness, which arises from the whole length of the anterior edge of the ridge of the preoperculum. The inferior fibres pass dorsad and cephalad, the superior and anterior pass ventrad and cephalad. The insertion is into the posterior edge of the peculiarly modified mandibular labial, and into a mandibulo-labial ligament, which also is peculiarly modified. The insertion into the bone is confined to a partially separated anterior bundle of fibres. The mandibulo-labial ligament is attached in front to the middle of the length of the maxillary labial as usual, and passes back to the muscle in a normal manner, but at the anterior margin of the muscle it is met by a tendinous band which passes ventrad and slightly caudad to be inserted on the outer surface of the mandible just in front of the Q-M. joint. The greater part of the upper fibres of the muscle are inserted into the normal part of this ligament, the lower fibres being inserted into the peculiar ventral limb.

Epibulus.—Although the single temporo-massetericus is here not a large muscle, it has a relatively more extensive origin from the reduced preoperculum. The muscle passes cephalad and ventrad to be inserted into a mandibulo-labial ligament, short and normal in its upper portion, but with a much elongated ventral limb inserted onto the outer surface of the mandible, as in *Drepane.*

Tandanus and *Cnidoglanis.*—The muscle has a fibro-tendinous origin from the usual edge of the preoperculum and from a similar raised subdermal edge of the hyomandibular above it. The tendinous fibres of origin penetrate the muscle and give origin to the muscle fasciculi, so that, though quite thin at its origin, the muscle rapidly becomes bulky. Contracting rapidly in front by the insertion of its fibres onto a deeply placed tendon, the muscle is inserted onto the internal surface of the articular above and lateral to Meckel's fossa, and onto the dorsal edge and outer surface of the bone above and external to the fossa.

The muscle is not divisible into anterior and posterior portions, but the deep tendon is in two definite strands.

Gadus callaris.—The temporo-massetericus in *Gadus* presents anterior and posterior parts. Holmqvist (1911) describes the pars anterior as the first, and the pars posterior as the fourth portion of the adductor mandibulae. This latter is completely fused, at its origin, with the underlying M. pterygoideus.

Amia.—The M. temporo-massetericus of *Amia* is that muscle which Allis described as the lower part of the superficial portion of the adductor mandibulae (A2′). It arises from the lower part of the subdermal edge of the preoperculum, and passes forward to be inserted, in part, into the ascending process of the lower jaw, but mainly into the mandibulo-labial ligament.

Polypterus.—(A) *Pars superficialis.* Quoting from Allis—"the superficial portion of the adductor mandibulae . . . has its origin in part on a line of tough connective tissue that is attached to the internal surface of the dorsal border of the cheek-plate, in part on the external surface of the dorsal portion of the hyomandibular and in part on the external surface of that part of the palato-quadrate that lies posterior to the ridge that runs upward across the quadrate from the outer end of its articular edge . . . The fibres of the muscle converge towards the ascending process of the splenial running antero-ventrally, anteriorly and antero-dorsally, and the dorsal and larger part of them are inserted on the dorsal edge of that process and along the internal surface of its hind edge, the ventral fibres passing directly into the ramus of the mandible and there being inserted on the internal surface of the dermarticular." This portion of the muscle lies entirely external to the ramus mandibularis trigemini.

(B) *Pars profunda.* The deep portion of the adductor mandibulae of Allis (1911). This arises from the quadrate in front of the origin of the temporo-massetericus pars posterior. Its fasciculi are inserted into a tendon which is inserted onto the dermarticular behind and below the insertion of the last part.

Innervation.—The ramus mandibularis of the Vth nerve maintains the constant relation to the muscle that we have observed in all the other bony fishes. It passes to Meckel's fossa between the temporo-massetericus superficial to it and the M. pterygoideus deep to it.

THE PTERYGOIDEUS MUSCLE.

Platycephalus (Fig. 27).—The muscle takes origin from the lateral surface of quadrate and os transversum, its postero-dorsal corner extending dorsad and caudad dorsal to the flange on the surface of the latter bone and, in this position, under cover of the levator arcus palatini. The muscle is relatively bulky and it is penetrated by a bipartite tendon into which its fasciculi are inserted, and which, in turn, is inserted onto the inner surface of the articular behind and below the insertion of the pars posterior of the M. temporo-massetericus.

Innervation.—This is by the mandibular ramus of the Vth nerve which comes into view from under the anterior margin of the levator palatini. Its direction is laterad and cephalad along the outer surface of the anterior edge of the os transversum. It passes superficial to the anterior end of the quadrato-mandibularis and enters Meckel's fossa between the tendons of this muscle and of the temporo-massetericus.

Anguilla (Fig. 26).—The muscle arises from the edge of the skull and from the anterior curved surface of the post-orbital bone. It is a relatively small, oblong, flattened muscle which passes from its origin ventrad with an inclination cephalad and laterad to be inserted into the articular below the fossa and internal to the insertion of the pterygoideus.

Innervation.—This is by the mandibular ramus of the Vth nerve. The nerve issues from its foramen in the cranial wall beneath this muscle and runs forward and laterad to appear in front of it just at the outer edge of the palato-pterygoid bone. It passes from sight by burrowing into the pars dorsalis of the temporo-massetericus just anterior to its tendon. It then turns ventrad and comes to lie posterior to the tendon and, running parallel therewith, it finally enters Meckel's fossa below the insertion of the temporo-massetericus tendons.

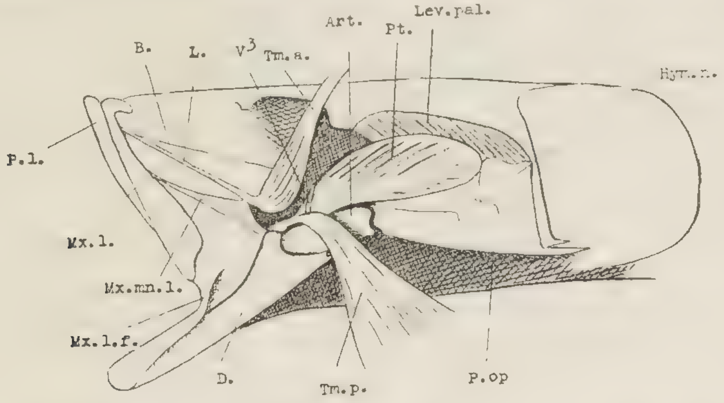
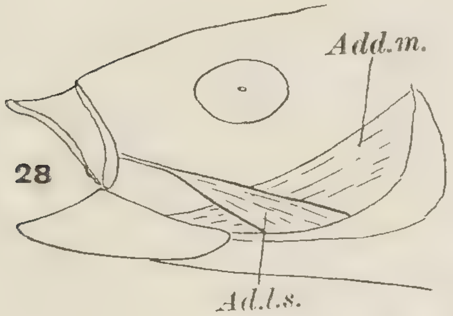


Fig. 27.—*Platycephalus.* The mandibular adductor muscles. Art., The articular bone; B., The line of attachment of the maxillo-labial fascia to the cranial base; D., The dentary bone; L., A separate slip of the maxillo-mandibular ligament; Hym.n., The hyomandibular bone; Lev.pal., The M. levator arcus palatini; Mx.l., The maxillary labial bone; Mx.l.f., The maxillo-labial fascia; Mx.mn.l., The maxillo-mandibular ligament; P.l., The premaxillary labial bone; P.op., The preoperculum.

Mugil (Fig. 28).—The pterygoideus is relatively a very massive muscle in this genus. It arises from the whole of the lateral surfaces of the quadrate, os transversum, and hyomandibular, and from a narrow submerged area of the preoperculum. The fasciculi are inserted into the strands of a brush-like tendon which penetrates the muscle. The point of the tendon "brush" is inserted into the articular behind Meckel's fossa.

28



29

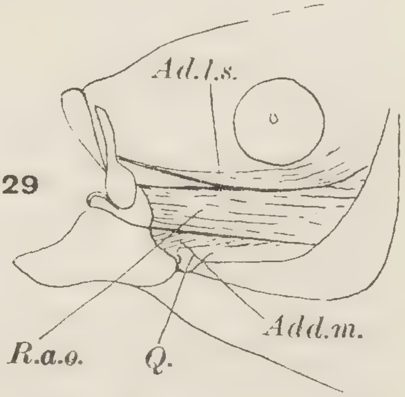


Fig. 28.—*Mugil.* Mandibular adductor muscles.
Fig. 29.—*Girella.* Mandibular adductor muscles.

Innervation.—From the mandibular ramus of the Vth nerve. This may be observed passing across the posterior wall of the orbit from its point of issue from the cranium, laterad and ventrad, and then laterad and cephalad. It crosses the superior surface of the butt of the pterygoid just at the boundary of the muscular portion and commencement of the bare portion of the short tendon of insertion, it then passes deep to the temporo-massetericus muscle and turns forward into Meckel's canal under cover of temporo-massetericus and upon the tendon of the pterygoideus.

Girella (Fig. 29).—The muscle in this genus is smaller than in the preceding, and is largely covered by the two portions of the temporo-massetericus. The origin is from the outer surfaces of the quadrate, hyomandibular and os transversum. The insertion of the fasciculi is into a tendon which is placed deeply and dorsal to most of them, and which, contracting to a relatively broad ribbon, becomes bound to the inferior edge of the tendon of the pars anterior of the temporo masseterieus and then is inserted along the inferior margin of Meckel's fossa.

Innervation.—Here the mandibular ramus of the Vth nerve issues from beneath the anterior margin of the levator palatini muscle and, turning ventrad, passes superficial to the tendon of the pterygoideus just behind the point of binding to that of the temporo-massetericus pars anterior. It then runs forward, deep to the tendons of the last muscle, parallel with and on the surface of that of the pterygoideus and enters Meckel's fossa.

Zanclistius.—The muscle here appears peculiar because the marked forward inclination of the suspensorium of the lower jaw has thrown the posterior limit of the muscles of mastication beneath the centre of the orbit instead of, as in the majority of the bony fishes, behind the orbit. The origin is from the outer surfaces of the quadrate, hyomandibular preoperculum, and os transversum. The muscle tapers as it passes cephalad and ventrad to its insertion onto the articular behind and above Meckel's fossa. There are three readily separable parts of this muscle. A superficial, which arises from the preoperculum, a deep, which arises from the hyomandibular and quadrate, and a ventral portion, which arises from a very short line at the extreme inferior and anterior end of the subdermal ridge of the preoperculum. The two former portions are flat and placed one beneath the other ; each has a deep tendon into which its fasciculi are inserted. The two tendons are intimately bound together in front of the fasciculi and are also bound to the tendon of the temporo-massetericus. The little ventral portion has an insertion free from the other parts below and behind them.

Innervation.—The mandibular ramus of the Vth nerve runs forward across the floor of the orbit and then cephalad and laterad on the surface of the levator palatini muscle along the dorsal edge of the pterygoideus for half the length of the muscle. It then crosses this last muscle under cover of the temporo-massetericus and turns mediad behind and below the inferior margin of that muscle at its insertion and, reaching the inner surface of the dorsal edge of the articular, passes down and forward to enter Meckel's canal.

Drepane.—The pterygoideus is here an extensive thin, flat muscle which arises from the bones of the suspensorium along their line of suture with the preoperculum. The anterior fibres pass almost directly ventrally, the posterior, or inferior, fibres pass cephalo-dorsally. They all converge to be inserted along the lower margin of Meckel's fossa.

Innervation.—The mandibular ramus of the Vth nerve passes downward and forward across the outer surface of the pterygoideus and under cover of the co-extensive temporo-massetericus to enter Meckel's fossa between the insertions of the two muscles.

Epibulus.—In this rather bizarre fish the pterygoideus is a relatively small muscle which arises from the hyomandibular and os transversum high up and deeply under cover of the levator palatini. The muscle is irregularly quadrilateral in section. It passes cephalad and slightly lateral and ventral, lying immediately below the orbit in front of the levator of the palatal arch, to the transverse level of the front of the orbit. At this point it terminates abruptly in a fine tendon which, bound to the maxillo-labial fascia, turns sharply ventrad and caudad to be inserted into the dentary just in front of the Q-M. joint.

Innervation.—Immediately after it passes laterad from the floor of the orbit the mandibular ramus of the Vth nerve passes over the pterygoideus and below deep to the temporo-massetericus and then runs downward and backward parallel to and between the tendons of the two muscles.

Tandanus and *Cnidoglanis.*—The pterygoideus in these two fishes is a solid muscle which arises from the hyomandibular and metapterygoid. It is clad on its anterior and superficial edge by a tendon into which its fasciculi are inserted. This tendon is inserted into the inferior and posterior margin of Meckel's fossa. An interesting little bundle of fibres arises from the free surface of the tendon close to the insertion and is inserted directly into the articular in front of the insertion of the tendon.

Innervation.—The mandibular ramus of the Vth nerve is here like all other nerves in these fishes, of a truly remarkable size. It passes down and forward under cover of the temporo-massetericus along the upper edge of the pterygoideus, crosses this last just before its insertion, and enters Meckel's fossa between the two tendons.

Amia.—I include as parts of the M. pterygoideus, the first, second and third parts of the levator maxillae superioris of Allis, the major portion of that which he designates the superficial part of the adductor mandibulae and his deeper portion of the same muscle.

(A) *Pars anterior.*—This is that which Allis describes as the third part of the levator maxillae superioris. It arises from the lower part of the edge of the prefrontal and contiguous part of the maxilla close to its posterior edge. The muscle is relatively short and flat, and ends abruptly in a slender tendon which is inserted above Meckel's fossa onto the ramus of the lower jaw.

(B) *Pars medialis* (Lms.[1], Lms[2] of Allis). This muscle arises in a situation closely similar to the single part of the pterygoideus in *Epibulus* and, in general, corresponds to that portion of the muscle which, in many of the bony fishes, arises under cover of the levator palatini from the upper end of the hyomandibular. The forward extension of the levator of the palate in *Amia* gives this part of the pterygoideus an unique appearance, which is, however, not in any sense truly peculiar.

(C) *Pars posterior* (Add_2'' and Add_2''' of Allis). This arises from the outer face of the preoperculum dorsal to the origin of the pars posterior of the temporo-massetericus, and from the lateral surface of the skull behind the orbit.

(D) *Pars profunda* (A_3 of Allis). This arises from the outer surface of the hyomandibular, below the levator palatini, and the outer surfaces of the quadrate and metapterygoid. These two parts of the muscle are strictly comparable with the two major portions of the muscle in *Zanclistius*.

Insertion.—The fasciculi of all three parts are inserted into tendons which arise in brush-like fashion within each part. These tendons are bound together close to the ramus of the jaw and are attached to the ascending process and to Meckel's cartilage around, but mostly dorsal to and in front of, the entrance to Meckel's canal.

Innervation.—In *Amia*, as in the more modern Teleosts, the muscle is innervated by the ramus mandibularis of the Vth nerve. The exit of the nerve from the orbit is somewhat peculiar in that it passes out just under the roof of the orbit, instead of across the floor or around the posterior wall and then along the floor diagonally laterad and cephalad as in all the other fishes I have described. In passing from the orbit the nerve comes to lie on the anterior end of the pars anterior and crosses that to pass superficial to the pars medialis. At the upper edge of the temporo-massetericus it dips under that muscle and runs ventrad between it and the pterygoideus pars medialis and profunda, finally entering Meckel's canal between the tendons of the pterygoideus, on the inner side, and the temporo-massetericus above and lateral to it.

Polypterus.—Two portions of the muscle are recognizable.

(A) *Pars anterior* (musculus pterygoideus of Allis). This arises from the side wall of the skull ventral to and also in front of the main trunk of the Vth nerve. From this origin it passes laterad, ventrad, and slightly cephalad, to be inserted into the internal surface of the dermarticular, its tendon being bound not only to that of the temporo-massetericus pars anterior above and in front of it, but also to that of the pars profunda of the pterygoideus below and behind it.

(B) *Pars posterior.* This is the "temporalis" muscle of Pollard (1892) and Allis (1922). Quoting from the latter (p. 253), "The musculus temporalis has its origin from the ventral surface of the posteronotosphenotic, from the supraorbital band of cartilage, and from that part of the ventral surface of the frontal that roofs the supraorbital fontanelle, the surface of origin of the muscle extending forward to the transverse plane of the foramen opticum. From this long surface of origin, the fibres of the muscle run postero-ventrally, ventrally and antero-ventrally, and passing external to the rami ophthalmicus profundus and ophthalmicus superficialis trigemini, and internal to the rami maxillaris and buccalis trigemini, are all inserted on the external surface of a tendinous band which lies between it and the musculus pterygoideus and which gives insertion, on its internal surface, to the fibres of the latter muscle. This tendinous band passes internal to the ramus mandibularis trigemini, and, diminishing in width, is inserted on the internal surface of the dermarticular."

Review.

There are a few mandibular muscles, such as the protractor mandibulae and muscles of the barblets in the Siluridae, which are present in only a few fishes and which appear to throw no light on problems of general morphology. If we omit these peculiar or, it may be, simply aberrant, muscles there remain for review and comparison four mandibular muscles only: the levator arcus palatini, the dilator operculi, the pterygoideus, and the quadratomandibularis.

The primordium of the mandibular muscles, the mandibular muscle plate, divides, in both Elasmobranchs and bony fishes, into an upper and a lower portion (Edgeworth, 1911). In the Elasmobranchs the upper portion gives rise to the levator maxillae superioris and the constrictor.

In the bony fishes the upper portion gives rise to the levator arcus palatini and the dilator operculi. From the lower portion, in both groups, the adductor muscles of the jaws are developed, as well as the ventral constrictors ; these last we have already dealt with.

There are, in the bony fishes, no other derivatives of the upper portion of the mandibular muscle plate than the two just mentioned. We are, however, not able to state with confidence that the two are completely homologous with those derived from the same portion of the plate in the Elasmobranchs. Although the relation of the dilator operculi and its specialized slip, the spiracularis muscle, in *Polypterus* to the spiracle lends support to the idea that this is the homologue of the elasmobranch mandibular constrictor, it is not quite convincing. We may safely only conclude that either these are homologous with those or that the levator arcus palatini is homologous with the levator maxillae superioris, and the dilator operculi is a new muscle derived from it.

Edgeworth (1911) tells us that, in *Scyllium*, after the separation of the mandibular muscle plate into upper and lower portions, the lower portion forms the adductor mandibulae, and later gains, anteriorly, an additional origin from the suborbital cartilage, and further, that this anterior portion of the adductor separates later, forming the levator labii superioris or adductor β of Vetter, the pterygoideus of this work.

He says of the development of the adductor mandibulae in the bony fishes, that . . . " at first passing from the palatoquadrate to Meckel's cartilage, it undergoes various changes in the specimens examined . . . In *Lepidosteus*, *Amia* and, probably, *Polypterus*, the adductor divides into internal and external portions . . . In *Amia* the internal portion sends forwards a projection from its upper end which forms the muscle connected with the olfactory chamber, the levator maxillae superioris portion 4 of Allis ". Still later " the remainder of the internal portion extends upwards above the level of the palatoquadrate and divides into three parts ". These are the remaining portions of the levator maxillae superioris of Allis.

If, as Edgeworth suggests, the adductor muscle primordium in *Polypterus* divides into internal and external portions, then it would appear that the pterygoideus of Edgeworth, Allis and Pollard, and the temporalis of the same authors, must be derivatives of the internal portion, and those muscles will be homologous with the derivatives of the same portion in *Amia*. I have designated these muscles the partes anterior and posterior of the pterygoideus respectively.

Now it is clear from Edgeworth's account that the pterygoideus of the Elasmobranchs and the pars anterior of the pterygoideus in these two bony fishes are developed in a very similar manner from similar portions of the adductor muscle primordium, although it also appears from the same account that the pars anterior anlage of the pterygoideus does not grow forward as in the Elasmobranchs, but is developed a little later from the deeper layer of the general primordium and extends upward.

Reviewing briefly the adductor muscles of the bony fishes : The temporo-massetericus may be present in one or in two portions which may be quite separate or may be fused to very varied degrees. Of these parts the anterior may arise from the skull in front of the orbit (*Amia* and *Polypterus*) from the skull behind the orbit (*Anguilla*) and/or from the bones of the suspensorium (the majority of the bony fishes). The posterior part arises from the bones of the suspensorium.

The pterygoideus may be present as a single more or less massive muscle, or may be more or less completely divided into two, three, or more portions which are more or less fused, one with the other. Of these various portions, one arises from the hyomandibular under cover of the levator arcus palatini, a second arises deeply from the bones of the suspensorium, whilst a third, more or less co-extensive with the last, arises from the same series of bones behind it and passes forward superficial to it.

The relation of the mandibular ramus of the Vth nerve, carrying the sensory fibres for the skin area immediately behind the symphysis of the lower jaw, to these two muscles is absolutely constant ; it is always superficial to the pterygoideus and deep to or posterior to the temporo-massetericus. In other words the former muscle is always crossed by or lies behind the sensory nerve in question whilst the latter passes superficial to or lies in front of the nerve.

This relation of the nerve to the muscles is the same as that which we observed in the Elasmobranchs, and, so far as the pars anterior in *Amia* and, presumably, *Polypterus*, their development is the same.

We may say with a great deal of confidence that the pars anterior of the pterygoideus muscle in *Amia* and *Polypterus* is homologous with part, at least, of the pterygoid muscle of the Elasmobranchs.

The situation of the pars posterior of the pterygoid in *Polypterus* (temporalis muscle of Allis), deep to and crossed by the maxillary and ophthalmic rami of the fifth nerve, may appear to be evidence against the statement in the preceding paragraph. I would remind readers that such a relation to those nerves is presented by the pterygoideus muscle in *Pristiophorus*.

As noted by Edgeworth, Pollard (1892) regarded the pars anterior of the pterygoideus (pterygoideus of Pollard) as well as the pars posterior of the pterygoideus of the Elasmobranchs. Edgeworth says that neither of them can possibly be homologous with that.

It probably needs no argument to establish the complete homology of the pars posterior of the temporo-massetericus throughout the bony fishes, but it is not so obvious that the pars anterior of the modern Teleosts is homologous with that of *Amia* and *Polypterus*.

The evidence in favour of this is, admittedly, not entirely convincing. It is, however, believed that the constant relation to the nerves and constancy of function as the retractor of the upper lip are important pieces of evidence in support.

The dissection of the many forms I have been fortunate enough to obtain has convinced me that the two portions of the muscle throughout the bony fishes are truly pterygoid muscles, and the following is advanced in support, and also as explaining how the conviction has arisen.

It is believed that there is no room for doubt that the pterygoideus muscle in *Rana* and *Amblystoma*, or indeed the Amphibia generally,is completely homologous with that of the Dipnoi. Again there is little reason to doubt that the muscle in, e.g. *Ceratodus*, is homologous with that of the Holocephali. That the muscle in *Callorhynchus* or *Chimaera* is homologous with that of the Selachii seems amply and convincingly proven by comparison with that of such forms as *Chiloscyllium*, *Pristiophorus*, and *Mustelus*.

Here is proof that, in the Amphibia, the muscle has acquired an origin behind the orbit, and in acquiring that origin it has maintained the relation to the submental terminal branch of the sensory components of the mandibular ramus of the Vth nerve.

It is its origin behind the orbit that alone raises doubts as to its homology with the pterygoideus muscle in the Elasmobranchs.

The doubts which arise from this factor are, however, to a large extent dispelled by consideration of the varying position of their origins relative to the orbit which the adductor muscles exhibit amongst the Teleostei.

In *Balistapus* (Fig. 29*a*) and its allies not only the temporo-massetericus, but also a part of the pterygoideus, arises anterior to the orbit. In *Gonorhynchus* (Fig. 29*b*) and a number of other fishes the origin is from the inferior margin of the orbit, from one of the suborbital scutes. In *Girella* and very many other typical acanthopterygian genera the origin of the muscles is from the cranium behind the orbit (Fig. 29*c*). Finally, in a very large number of the Teleosts, the origin of the temporo-massetericus is from the hyomandibular, quadrate or preoperculum. *Mugil* may be accepted as exemplary of this last group (Fig. 29*d*).

In view of the fact that the temporo-massetericus muscle has, very definitely, its origin anterior to the orbit in some Teleosts and, just as definitely, behind it in others, it seems that one may, quite reasonably, accept the view that in similar manner the pterygoideus has acquired an origin behind the orbit in the tetrapods.

In conclusion it may be stated that in the Cockatoos the pterygoideus has its origin in front of the orbit.

THE INNERVATION OF THE EYE MUSCLES.

After discussing the serial homologies of the muscles of the hyoid and mandibular arches it is desirable to endeavour to understand the fate of the dorsal portion of the mandibular and hyoid muscle-plates. These, in certain of the vertebrates, are intimately related to the development of the rectus externus and oblique superior eye muscles.

v. Wijhe (1882), and later Neal (1914), regarded the eye-muscles as remnants of the trunk myotomes of the premandibular, mandibular hyoid segments, or at least of the myotomes anterior to the auditory.

Whilst agreeing with this interpretation I find myself unable to accept v. Wijhe's interpretation of the IV, V, VI and VII nerves. Edgeworth also has offered an interpretation of these nerve muscle associations, and this too I find unsatisfying.

I have tabulated below the history of the development of the eye-muscles in the different vertebrate groups. Their innervation needs no tabulation.

Following that tabulation I offer still another interpretation of the facts.*

The eye muscles are developed from :

the first three myotomes in	the first two in	the first only in
	Teleostomi	Dipnoi
Plagiostomi		Urodeles
	Sphenodon	Anura
	Lacertilia	
	Ophidia	
	Chelonia	
		Monotremata
		Marsupialia
		Mammalia

These facts may be presented with more detail as follows :

	Superior, inferior and external and inferior oblique recti.	Superior oblique.	Internal rectus.
	are developed from the :		
Plagiostomi	P	M	H
Acipenser	P	M	M
Amia	P	M	M
Lepidosteus	P	M	M
Dipnoi	P	P	P
Urodeles	P	P	P
Anura	P	P	P
Sphenodon	P	M	M
Lacertilia	P	M	M
Ophidia	P	M	M
Chelonia	P	M	M
Monotremata	P	P	P
Marsupialia	P	P	P
Mammalia	P	P	P

P=premandibular somite. M=mandibular somite. H=hyoid somite.

The interpretation I would offer of these facts is as follows :

Primitively the eye-muscles were but four in number, all developed from the premandibular somite, and innervated by the third nerve, which was the proper motor nerve of the segment. Later, as a result of the extreme flexion of the head, brought about by the unequal growth of the brain segments, this first myotome was brought close to the second and third myotomes dorsally. They were in this situation crowded together and two extra eye-muscles were developed from the contactual apices of these other two myotomes and they were innervated by branches of the third and fourth segmental motor nerves, namely the V and VII.

---

* In approaching this question I am quite unable to accept Edgeworth's dictum—" that no theory (explaining the development of the eye muscles) will be found satisfactory which does not also take into account the phenomena in Dipnoi, Urodela and Ganoids and this without any underlying supposition that the conditions in Selachii are necessarily the most primitive, and others found are modifications of them ".

Professor Edgeworth has, like myself, devoted many years to the intensive study of the anatomy and development of the vertebrate head, and our writings indicate that we are neither of us prepared to be bound by accepted opinion, but are distinctly radicals in the field we have chosen. It is, therefore, interesting to observe that very similar lines of study should have led us to adopt such different attitudes on this fundamental question. It serves to illustrate very forcibly how important a factor is the personal in any equation which attempts to set forth evolutionary values.

Confining myself to the field in which I have toiled most assiduously, I would point to the very generalized condition of the wholly cartilaginous skull, the simplicity of the nasal and auditory capsules, the simplicity of the brain itself, and especially of the prosencephalon, and finally to the generalized form of the branchial and masticatory frameworks and their musculature. When to these there be added the geological antiquity of the Elasmobranchs, undoubtedly greater than that of any other vertebrates, it seems to me that it were little short of unreasonable not to regard them as more primitive, more nearly reflecting the anatomy and development of the common ancestor of all vertebrates, than any other form available for study today.

One looks forward with interest to reading a detailed exposition of the factors of anatomy and embryology that led Professor Edgeworth to adopt the view he does.

When, later in development, the head was straightened out, the main body of the mandibular and hyoid muscle-plates became completely divorced from the small apical portion. Whilst the main mass resumed its original position, the apical portions retained the new. At the same time there was a relative backward movement of the motor nerve nuclei within the brain. In the result there has been in each generation a relative pull forward on the motor twigs of V and VII, supplying these new eye muscles, which pull is assumed to have brought about the relative forward movement of the nuclei of those twigs, producing nerves IV and VI.

The development of the eye-muscles in the Plagiostomi completely explains the presence of three motor nerves. Though there is lost to us the stage in which the two newer muscles are related to the other muscle-plates in the higher vertebrata, the three nerves clearly indicate the plurality of origin and prove that the embryonic plate in these forms is a composite one.

The conditions in the Teleostomi and the Reptilia present an intermediate stage in which the apex of the hyoid myotome has been, as it were, transferred to the mandibular before tissue differentiation permits of its detection. The fusion of the apical portion of the mandibular and premandibular myotome is the only trace left of the transference of the two dorsal buds together in the development of the muscles in the Amphibia.

The developmental history of the eye-muscles in the Plagiostomes *per se* does not explain the extra motor nerves in certain of the brain segments in front of the auditory vesicle. That explanation is offered by my proposed interpretation of the facts, and it simplifies the problem of the reconciliation of brain and head segments. There would be, according to this interpretation of mine, only three segmental motor nerves in the three segments of the brain in front of the eighth: the premandibular (III), the mandibular (V), and the hyoid (VII).

Both V and VII are to be regarded as having each a branch which has a course entirely independent of the rest of the nerve, namely the IV and VI nerves.

Here, is neither time nor place to enter on an extended discussion on the segmentation of the head and brain, but it is permissable to point out that there are unique features in the generally accepted interpretation of just these neuromeres and their related somites. According to that interpretation these somites differ from all the other somites in the body in that they possess completely independent somatic and visceral motor nerves. Here, are two somites provided with four motor nerves and for two of these nerves, IV and VI, there are no corresponding sensory nerves. Moreover, it is not possible to regard the motor components of V and VII as entirely visceral, for they innervate some muscles which are neither anatomically nor developmentally visceral. This introduces the further anomaly that though one of the motor nerves to each somite is a mixed visceral and somatic nerve, there is yet another somatic motor nerve to each of the somites.

These conclusions may be presented in tabular form:

Neuromere ..	I	II	III	IV	V	VI	VII
Somite ..	?	?	?	?	Pre-mandibular	Mandibular	Hyoid
Motor nerve					III	V+IV	VII+VI
Sensory nerve					Ophth. prof.	V	VII

THE SKULL IN THE ELASMOBRANCHS.

In the head skeleton or skull several distinct entities are more or less closely knit together. They are: 1, the brain capsule, or cavum cranii,* 2, 3 and 4, more or less complete capsules for the lodgement of the three paired organs of the special senses of sight, hearing and balance and of smell, 5, a series of paired and unpaired fused and/or articulated elements related to the jaws and palate and serving the function of mastication, and 6, a series of paired jointed rods which together constitute a set of branchial or visceral arches related, primarily, to branchial respiration.

---

* The term cranium has been used generally to designate the brain and auditory capsules; it is impossible, owing to their intimate fusion, to describe either of these separarely in the great majority of instances, because the inner wall of the one is so commonly the outer wall of the other. It is in this sense that the term will be used throughout this work. On the other hand the designations chondrocranium and primordial cranium are usually used to include all the components of the embryonic cartilaginous head skeleton, and with that general application the terms will be used in this work. In some instances, more particularly primitive forms, the description and/or illustration of a cranium will of necessity also include the nasal capsules. The term cavum cranii is used to indicate the brain case only.

Of these various entities the auditory or otic capsule, which lodges the organ of hearing and balance, is always attached to and incorporated with the side wall of the cavum cranii towards its hinder end. The nasal capsules, situated in front, are also always attached to the cranium, and with it form part of a cartilaginous or bony continuum. The attachment is more direct and intimate, in the cartilaginous skull, in the more primitive forms. Whilst these two capsules more or less completely enclose their respective organs, the optic capsule is relatively incomplete. In cartilaginous skulls it is commonly but a bay or recess between the other two capsules in front and behind and the cranial wall medially. To these, more or less adventitious walls, there are added more or fewer flanges or processes, which more or less completely enclose the organ, except, of course, on its outer aspect. The optic capsule or orbital socket is, generally speaking, more complete in the bony than it is in the cartilaginous skulls.

In addition to the above six entities there are in many primitive skulls certain paired labial skeletal elements related to the outer aspect of the anterior masticatory components and nasal capsules. Further there are incorporated with the hinder end of the cranium more or fewer vertebrae. In some cases this incorporation is of such a kind that the vertebral origin and nature of the incorporated portion is quite obvious; in others the original character of the vertebrae is entirely lost, and the evidence of the incorporation has to be sought, not in cranial morphology, but in the relation of certain nerve roots to the cranial wall.

It is desirable that a discussion on the form of the adult cartilaginous skull should open with a description of the most generalized type available. Such a form is presented by almost any typical Selachian. Our illustrations are based on the skull of a five foot specimen of *Carcharias arenarius* Ogilby (Figs. 30, 31, 32 and 33).

The cranium of this Selachian is a continuous cartilaginous structure, in which one recognizes at once the large auditory capsules incorporated into the side wall posteriorly and the outstanding nasal capsules in front. Between these two the orbital recess is very imperfectly converted into an optic capsule by a laterally projecting horizontally flattened ant-orbital process, a rod-like, downwardly projecting post-orbital process which terminates below in a bifurcation, and a more or less incomplete floor, the suborbital process.

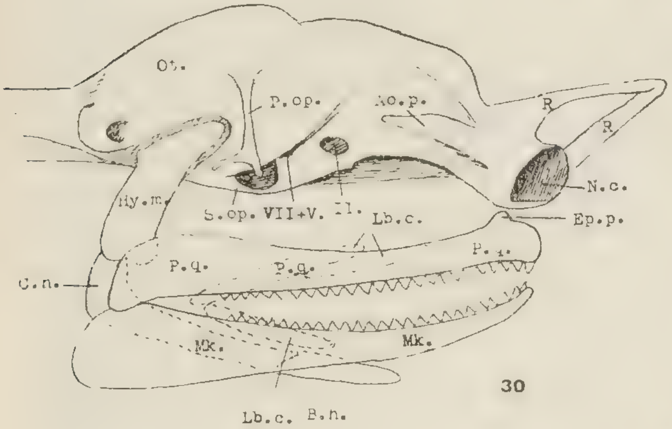
The brain capsule itself presents no division into parts or regions, but is a continuous cavity of varying size. Narrow behind, where it communicates with the vertebral canal, it becomes enlarged as it extends forward, and is widely open in front. Just in front of this wide anterior opening of the cranial cavity, there are, on each side, the medial apertures of the nasal capsules. These last are relatively simple, somewhat barrel-like structures having an opening medially towards the cranial cavity, and another, at the other end of the barrel, which is directed forward and down. A rostral process, developed to a variable extent in all Elasmobranch skulls, is represented in our example by one ventral median and a pair of dorsal processes which are all three united together anteriorly.

Although the cranium is not divided into regions, there are certain perforations in its side wall and a fossa on its floor to which we must pay particular attention, because they are important landmarks. These perforations are the foramina of exit of the cranial nerves, and of ingress of the main cerebral artery. The fossa is the sella turcica or pituitary fossa and lodges the hypophysis cerebri. These foramina and this fossa and the structures which they lodge or transmit bear very constant relations throughout the whole vertebrate series to both brain and skull areas and components. They are therefore trustworthy and reliable features on which to base identifications of these skull areas and components.

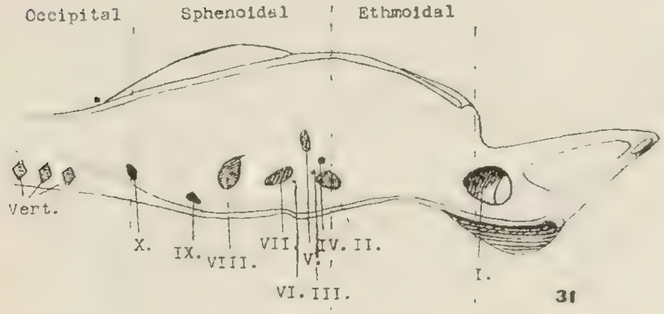
By the pituitary fossa the cranial cavity is clearly marked off into "prechordal" and "chordal" or "parachordal" areas, the former lying in front of the anterior end of the notochord, the latter behind that point. These, it will be found, are exceedingly important divisions of the cranium.

On either side of the pituitary fossa in, or close to, the floor of the cranium will be found the two carotid foramina. These admit to the cavity the terminal cerebral branch of the internal carotid artery. Their position is remarkably constant throughout the whole of the vertebrates, and they are of prime importance as assisting us to recognize the homologies of certain related structures.

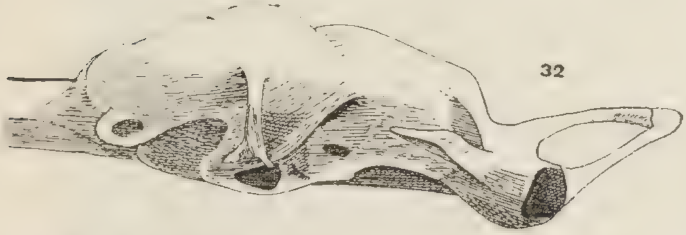
Of the nerve foramina present in our example, the more important are those for the second, fourth, fifth and seventh together, eighth, ninth and tenth. The smaller apertures for the third and sixth nerves are not of comparative craniological importance in the more primitive skulls.



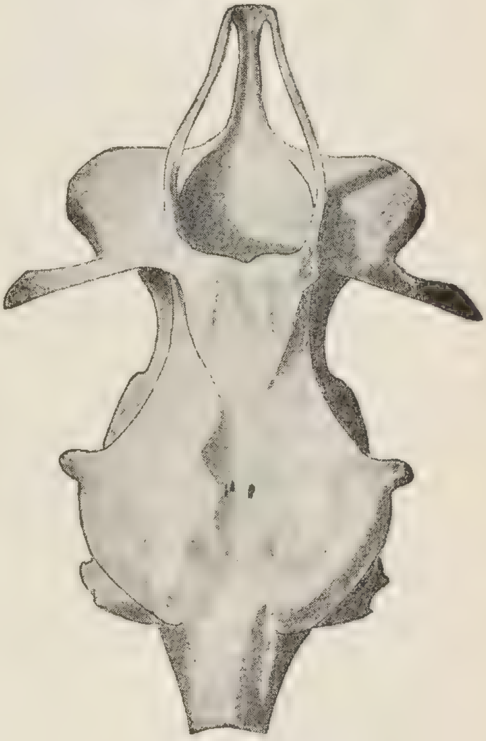
30



31



32



33

Figs. 30, 31, 32, 33.—*Carcharias.* Ao.p., Antorbital process; B.h., Basihyal; C.h., Ceratohyal; Ep.p., Ethmoid process; Hy.m., Hyomandibular cartilage; Lb.c., The labial cartilages, indicated by dotted lines; Mk., Meckel's cartilage; N.c., Nasal capsule; Ot., Otocrane; P.op., Postorbital process; P.q., Palatoquadrate; R., Rostrum; S.op., Suborbital process; Vert., Intervertebral discs; I-X, The foramina for the cranial nerves.

The external apertures of the second, third, fourth, fifth, sixth and seventh nerve foramina will be found on the inner wall of the orbital recess, that for the fifth and seventh being the most posterior and situated just in front of the otic capsule. The foramen for the eighth, the auditory, nerve perforates the inner wall of the otic capsule. That for the ninth emerges just behind that capsule and the tenth is placed still further back. In addition to the above foramina there is present a special foramen for the transmission of the superficial ophthalmic branches of the fifth and seventh nerves. This is situated above and in front of the other foramen for those nerves.

When the otic capsule is entered, it is found to be incompletely divided into compartments which lodge the three semi-circular canals, the sacculus and the utriculus, portions of the auditory organ.

The anterior aperture of the cranial cavity is known as the anterior cranial fontanelle ; it is present in the majority of elasmobranch crania. In the flesh it is closed by a tough membrane which is attached to the side walls and floor in front of the internal apertures of the nasal capsules, which are designated the olfactory foramina.

The nerve foramina are designated for the most part by the nerves they transmit. Thus the second nerve leaves the cranium through the optic foramen, the fourth through the oculomotor foramen, and so on. The foramen for the exit of the main branches of the fifth and seventh nerves is an exception to this rule. There is a good deal of variation in the composition of the nerve trunks which, in the different classes, pass through it, and, moreover, its position immediately in front of the otic capsule is one of such constancy and importance to the student of homologies that it has been designated the *foramen prooticum*. It will be found that in certain forms the prootic foramen is converted into a prootic notch, *incisura prootica*, by the absence of a complete front wall, and cranial roof above it.

For descriptive purposes the cranium may be divided into three regions known respectively as the occipital behind the vagus or tenth nerve foramen, the sphenoid between the vagus and optic foramina, and the ethmoid in front of that last foramen. These names have been derived from certain bones which are constantly related, in bony crania, to the respective areas, and although the bones in question are, some of them, variable in their extent, and indeed at times invade regions both behind and in front of their own proper spheres, still the designations have for the student of comparative craniology very definite applications and are as useful as definite.

The skeletal structures of the skull related to the function of mastication and those related to the branchial basket together constitute the seven visceral arches.

The first visceral arch is the mandibular, or more correctly the maxillo-mandibular. It presents on each side dorsal and ventral halves. The dorsal is variously designated the palato-pterygo-quadrate, the palato-quadrate, and the sub-ocular arch. The ventral half is the mandibular arch, using that term in its restricted sense, or Meckel's cartilage.

The second is known as the hyoid arch, also divided on each side into dorsal and ventral halves ; the upper half is the hyomandibular and the lower commonly designated the hyoid bar, but which commonly is divided into upper, ceratohyal, and lower, hypohyal, portions. The hypohyal elements of the two sides are united to a median ventral basi-hyal or hyoid copula.

The remaining five arches are the branchial arches, each divided on both sides into four segments ; from above down these are pharyngo-, epi-, cerato-, and hypo-branchial cartilages. As in the case of the hyoid arch, so in each of the branchial arches, the ventral segments of the two sides are united to a median ventral basibranchial. More or fewer of the basibranchials may be united into a continuous basibranchial plate. The posterior basibranchial is commonly prolonged posteriorly and has been designated the cardio-branchial, in recognition of its relation to the heart.

The branchial arches are loosely slung to the skull, for the most part by muscular attachments only. The hyomandibular cartilage is, on the other hand, firmly, though movably, articulated to the inferior surface of the otic capsule. Its inferior end is similarly bound to the posterior end of the palato-quadrate cartilage, either directly or, in the Chondrostei, by the intermediation of a little symplectic cartilage ; it is also bound to the upper end of the ceratohyal cartilage.

The palato-quadrate cartilage is firmly bound by a stout fibrous ligament, but without a true joint such as is present between the hyomandibular and the otic capsule, to the cranium behind and below the nasal capsules. This is known as the ethmo-palatine ligament, and may be attached to a similarly named process on the upper aspect of the palato-quadrate cartilage. The palato-quadrate is articulated posteriorly to the hinder end of Meckel's cartilage. The two cartilages together form the upper and lower jaws on each side. The jaw cartilages of the two sides are very firmly united in a median symphysis in front.

The labial cartilages are one, two, or three in number on each side, two enclosed in the upper lip and one in the lower. The anterior upper cartilage is commonly attached to the posterior, and this in turn may be attached by its posterior end to the posterior end of the lower labial cartilage.

In addition to the branchial elements mentioned above, there are commonly present a variable number of extra-branchial cartilages attached in varying modes to the separate arches. These extra-branchials are of taxonomic value, but are for the most part devoid of any significance to the student of the wider problems of homologies and of evolution.

Having described the skull of *Carcharias* in rather general terms we may describe that of one of the Rays, *Urolophus*, with more specific intent. It will serve as a second example of the "Selachian" type.

The cranium has a definitely dorso-ventrally compressed appearance. The three struts of the rostral process may be described as having been united by membranous sheets of cartilage so as to produce a trough-like rostral process, V-shaped in both cross and horizontal sections, and widely open above. The nasal capsules are very similar to those of the preceding form, but the ventral, external, aperture is so extensive that there is no floor. A curved flange of cartilage is attached along the inner half of the upper and posterior edge of the nasal capsule. This flange is nearly vertical but, with a slight backward lean, it swings round onto and then along the outer edge of the cranium above the orbit, it gradually inclines more into the horizontal plane and is continued right back along the outer edge of the otocrane, or otic capsule. There is a narrow suborbital flange attached to the lateral edge of the cranium inferiorly. This merges into a stouter lateral occipital process posteriorly. This last is surmounted by a little arch which springs from its outer edge and bends inward to be attached to the side wall of the cranium behind the otocrane.

The cavum cranii is not divided into regions, except in so far as such are indicated by the nerve foramina. The foramen prooticum is large, and in some of the Rays is divided into two. The internal auditory meatus, foramen for the eighth nerve, is placed low down, almost right in the angle between floor and wall.

The otocrane is small and compact. The nasal capsule is large.

There are no periorbital processes other than the flanges already described.

The visceral arches conform absolutely to the selachian type, but the ethmo-palatine ligament and process are not present. In the result the jaws have a greater mobility than have those of the Sharks. Certain of the muscles of mastication are especially modified to give purposive direction to this increased mobility, and the two jaws together with the lips are, by these muscles, capable of being bodily protruded. The Chondrostei closely resemble the Rays in these features.

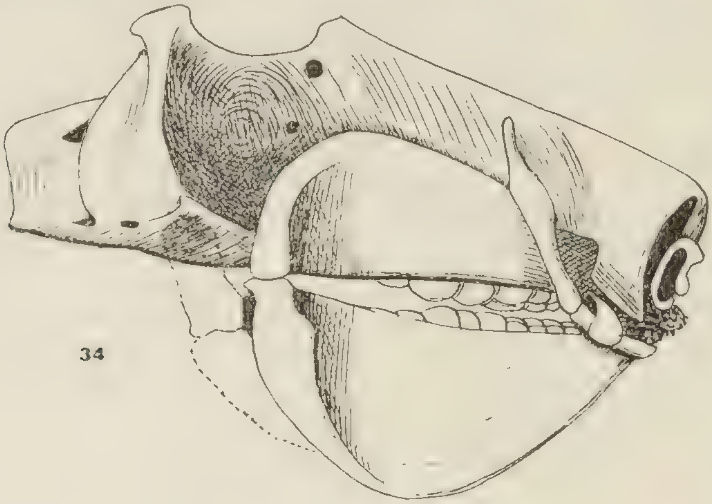
Heterodontus.

(Figs. 34, 35.)

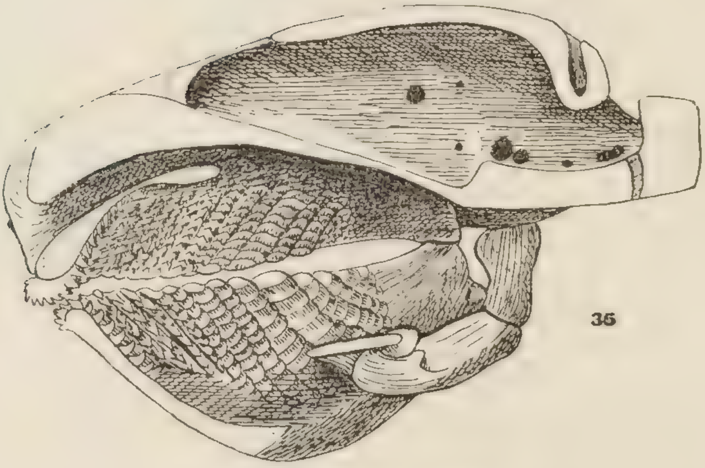
The skull of *Heterodontus portus-jacksoni* with the palato-quadrate in position presents a peculiar resemblance to the skull of the Holocephali. This resemblance is largely destroyed by the discovery that the upper jaw is not continuous with the cranium but only attached by an ethmo-palatine ligament more extensive than usual. Even so, there still remain marked resemblances. The orbit is placed relatively far back, as in the Holocephali, and masks the otocrane behind it, and further, as in these forms, the orbit is tolerably complete and well defined, with all the nerve foramina from the second to the seventh on its inner wall. There are two complete canals for the superficial ophthalmic branches of the seventh nerve in precisely the position of those canals in *Chimaera* and *Callorhynchus*. There is, however, no median dorsal crest to this skull, and the absence of the crest leaves the canals open dorsally.

The anterior cranial fontanelle lies in the horizontal plane; this is because the skull roof is carried forward on either side and forms an incomplete roof for the sphenoidal cavity in front of the cavum cranii proper. In front of the sphenoidal cavity the skull presents a peculiar resemblance to that of *Neoceratodus*. The roof of the nasal capsules is laterally expanded in the same plane as the roof of the sphenoidal cavity. The two together have the same triangular outline, as viewed from above, as the two nasal roofs in the Dipnoan, and they are similarly thin and fenestrated, the fenestrations being confined to near the front margin. A central furrow separates the nasal roofs of the two sides, and below this furrow there is placed the internasal septum. The furrow is continued right forward to the tip and then passes down and onto the inferior surface of the septum. The septum is as deep in front as it is at its origin behind. Inferiorly it bears, on either side, along its length, a narrow horizontal process which forms a very incomplete median nasal floor (solum nasi). The lateral margin of the nasal roof is turned down and forms a postero-lateral wall, of full depth, to the capsule. Anteriorly the ventral margin of this wall turns medially into the horizontal plane, resulting in the formation of an incomplete lateral area of nasal floor.

Each nasal cavity is, then, triangular as viewed from above or below. Two sides of the two triangles lie parallel, along the mid-line, the nasal septum. The bases of the triangles are forward and slightly outward. The angle which each forms with the mid-line is approximately 80°. The angle which the postero-lateral side forms is approximately 40°. Dorsal and ventral sides are nearly flat and in parallel planes. There is little of the anterior wall and very little floor; the other walls are complete. The vertical walls become concave towards the depth of the cavities, so that looking into the apex of the triangular cavity one observes a circular olfactory passage which opens directly into the sphenoidal cavity.



34



35

Figs. 34 and 35.—*Heterodontus*.

In *Gyropleurodus galeatus* Gill, the dorso-lateral margin of the sphenoidal and cranial cavities carries, on each side, a vertical ridge. Low in front, where it commences immediately above the olfactory passage, this becomes more elevated as it passes back. The two ridges incline towards one another as they pass the middle of the length of the sphenoidal cavity, and then diverge again as the brain cavity widens just in front of the orbit. Here the ridges incline outward and backward, forming the anterior boundary and roof of the orbit. They now approach one another rapidly and decrease in height. Then, bending abruptly outward, they merge with a similar flange which rises in the transverse axis of the skull from the antero-dorsal margin of the otocrane and incline forward over the back of the orbit.

The incomplete canals for the superficial ophthalmic branches of the seventh nerves lie on the roof of the sphenoidal cavity against the inner side of these ridges. The nerves in question enter the orbit relatively high up behind and, after passing forward against the inner wall, perforate the anterior wall to reach the canals exactly as they do in the Holocephali.

In *Heterodontus* the dorsum of the skull is much more simple. Commencing anteriorly, the broad triangular roof of the nasal capsule narrows behind and merges into a narrow horizontal shelf which contributes to the incomplete roof of the sphenoidal cavity. Behind that cavity the shelf widens both mediad and laterad, joining its fellow of the other side behind the anterior cranial fontanelle to form the complete roof of the cranial cavity proper and overhanging the orbit laterally. There is a narrowing again at the posterior boundary of the orbit, which is also the anterior boundary of the auditory capsule. Behind this point there is a marked widening of the dorsum, above the two auditory capsules. At the posterior limit of this capsule the dorsum gives place abruptly to the posterior (almost) vertical wall. The posterior slope is broken across the mid-line by a narrow pit into the depth of which there opens on each side the ductus endolymphaticus.

The side wall of the cranial cavity is very complete, the inner wall of the orbit is almost entirely cartilaginous, and there is a narrow membranous margin to the optic foramen, in place of the relatively extensive deficiency usually found in this region in elasmobranchian skulls. The pituitary fossa and post-clinoid eminences are obvious features on the floor of the cranium. The latter is, as it were, swung onto the side wall, and the rounded eminence that results forms the anterior boundary of the foramen prooticum. At the side of the floor of the pituitary fossa is the foramen oculo-motorius, and above and in front of this the optic foramen. Below and behind the foramen prooticum is a veritable meatus acusticus internus, with its internal facial foramen in front and the auditory foramen behind at its base. Behind this again is the relatively small glossopharyngeal foramen with the larger vagus foramen behind it.

On the lateral external surface of the skull, the last two passages lead out into relatively large glossopharyngeal and vagal fossae, which are situated on the infero-lateral and anterior corner of the capsule. At the infero-lateral and anterior corner of the capsule there is the large triangular joint buttress to which the head of the hyomandibular cartilage fits. Immediately above this, and formed by the strengthening flange of its upper margin, there is a broad shallow groove across the lateral and anterior edge of the capsule. This is the incisura venae capitis lateralis which is quoted in the text as the defined point in the description of the origin of certain of the hyoid and mandibular muscles. The orbit has very incomplete floor and roof, no anterior wall, but a complete posterior wall formed by the otic capsule. An antero-lateral wall is formed by the upper part of the palato-quadrate. The foramen prooticum externum is placed about the middle of the height of the orbital recess immediately in front of the antero-medial edge of the auditory capsule. Just below it is the external aperture of the facial canal. Just in front of it is the external aperture of the canal for the internal cerebral artery. This runs transversely beneath the investment of the front of the post-clinoid eminence and joins its fellow of the other side. Each gives off two branches: one as soon as the canal has penetrated the cranial wall—this is very short and opens at once through the fibrous investment; the other, just to one side of the centre line, runs ventrad against the clinoid wall under the fibrous investment and divides. One branch opens at once at the side of the pituitary body, the other passes through the pituitary fenestra. The external oculomotorius foramen is in front of the arterial foramen. Quite a large foramen in the floor of the orbit, in front of the external facial and below the oculomotorius, transmits the ramus ophthalmicus profundus VII.

Posteriorly the lateral edge of the floor of the orbit is a ridge; when this ridge, inclining medially, meets the side wall of the skull at the front of the orbit, it becomes converted into the lower wall of a groove which runs forward and mediad under the floor of the sphenoidal cavity to terminate beneath the posterior end of the olfactory canal. This groove is fitted by nearly the middle one-third of the upper edge of the palato-quadrate.

The nasal capsules have little anterior wall formed directly from the primordial cranium, but they have an adventitial anterior nasal cartilage which strengthens the anterior wall very efficiently. The nasal septum may be said to be split into two vertical halves just as the anterior end; these halves diverge and curve laterad, extending further inferiorly, then superiorly. The roof bends ventrad anteriorly, terminating in a narrow vertical fringe. As viewed from in front, the free edges of the nasal walls present a superior margin which slopes from the centre laterad and ventrad, and ends by curving mediad. The median margin is nearly vertical but with a slight inclination laterad. Inferiorly the margins do not meet. The peculiarly shaped adventitious nasal cartilage fits the outer curve of the edges and extends mediad in contact with the superior margin. About the centre of that margin it abruptly bends ventrad and mediad, leaving an unfilled triangular gap medially. The arm of the cartilage which bends mediad and ventrad is bifurcated; the larger arm is that which gives direction to the cartilage, and it is attached to the inferior and lateral corner of the out-turned anterior end of the nasal septum. The smaller arm curves around in the vertical transverse plane so as to complete half a circle and ends freely, turning back to the outer piece of the cartilage, which fits the outer curve of the capsular margin. This is also bifurcated, but in this instance the two arms are placed one behind the other. The posterior arm fits against the free ventral and median margin of the incomplete lateral nasal floor. The other, and lesser arm, projects forward somewhat close to, but free from, the laterally projecting small median arm. The cartilage as a whole then may be described as an incomplete hoop whose ends are bifurcated. This hoop surrounds the nasal aperture.

Callorhynchus antarcticus.

The skull of *Callorhynchus* has already been fully described and illustrated (Kesteven, 1933).

The Skull of the Chondrostei.

The development and adult form of the skull of the Sturgeon was described by Parker (1882). Bridge described the skull of *Polyodon* (1879). *Scaphyrhynchus* is essentially similar to *Acipenser*, and *Psephurus* as closely resembles *Polyodon*.

There are, then, two distinct types of recent chondrostean fishes' skulls and these, whilst fundamentally similar, present marked differences.

Gregory (1933) agrees with the view of Watson and Stensio, that the " partly cartilaginous condition is due to retrogressive development (perhaps to the retention of early larval conditions in the adult)". This last suggestion is, of course, quite contrary to the evidence. The early larval chondrocranium is a very incomplete, fenestrated structure, and it is only in late larval and early adult stages that the chondrocranium is completed. It is pointed out later that the complete cartilaginous skull is not a primitive character, but is the peculiar feature of the Elasmobranchii.

Probably the most important feature wherein these chondrocrania differ from those of the Selachii is the wide lateral cranial fenestra. In this they resemble the Holocephali and the bony fishes.

The nasal capsules, though much reduced in size, are essentially elasmobranchiate in character. They are not, as in the bony fishes, simple depressions on the dorsum of the ethmoidal cartilage but have the typical three complete walls of the sharks and rays and, in addition, a complete floor.

The rostrum is very similar to that of the rays and of such sharks as *Pristiophorus*. This is particularly so in *Polyodon* and *Psephurus*. In these two fishes the root of the rostrum is formed by two sloping narrow plates of cartilage. Each commences above and behind at the antero-lateral corner of the nasal capsule, just as in the plagiostomes, and meets its fellow at the mid-ventral line, forming, as in the Rays, an open V-shaped trough. This trough becomes shallower as it reaches forward, and as the superior edges draw toward the mid-line anteriorly its walls become thicker and, expanding laterally, form the long spathulate anterior portion of the rostrum.

There are, of course, no endochondral bones developed in the skull of either of the Polyodontidae, and the covering bones are, for the most part, of a very indeterminate character. The synpterygoid is the only bone whose identification is completely beyond question. It resembles that of the Dipnoi in that it extends posteriad well beyond the limit of the cavum cranii. Bridge described in *Polyodon*, and figured, a " vomer " suturing with the anterior end of the synpterygoid; there is no trace of this bone in my young specimens of *Psephurus*, nor do I find there any trace of the post-temporal of Bridge's description of the adult *Polyodon*. The lateral wing of the synpterygoid (" basi-temporal ala " of Bridge) is much larger in *Psephurus* than in *Polyodon*; it is not only wider antero-posteriorly, but extends higher on the lateral wall of the otocrane. The bone on the side wall of the cranium which Bridge termed post-temporal has been identified as the prootic by Gregory; this is obviously an incorrect identification. It cannot even be identified as a dermo-opisthotic, for it is placed entirely behind the otocrane.

The roof pattern.—In *Psephurus* there is a median splint which commences above the hinder limit of the cavum cranii and ends anteriorly a little in front of the transverse level of the anterior limit of the otocrane. Very narrow behind, the bone becomes wider in front and is bifurcated.

Between its bifid anterior end and overlapping it another splint is placed. This is almost as wide as the posterior splint where the two overlap between the two auditory capsules, but tapers to a very fine and long filament which runs forward well in front of the orbits.

Over the auditory capsules, on each side, there is a very thin scale resembling that which, in *Polyodon*, Bridge termed dermosphenotic, but differing in that its anterior and posterior lateral splint-like elongations are relatively much longer than in *Polyodon*. This bone is narrow over the capsule, but has quite a long suture with both the median bones per medium of anterior and posterior median splints similar to the lateral but not nearly so long.

The roof pattern of *Polyodon* differs markedly from that of *Psephurus* as I have just described it; whether this is due to the juvenility of my material I am not in a position to say. In *Polyodon* Bridge described a median posterior bone which he termed parietal, suturing in front with paired frontals, and between these a single bone which he called the dermo-ethmoid; lateral to the parietal and suturing with it a dermo-sphenotic; behind this a dorsal splint from the post-temporal, and, suturing with it in front, a splint which he terms nasal or dermo-prefrontal (Fig. 36).

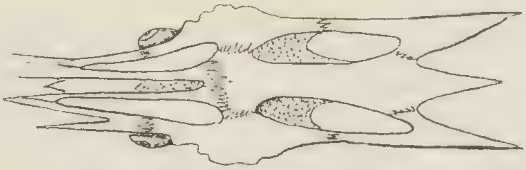
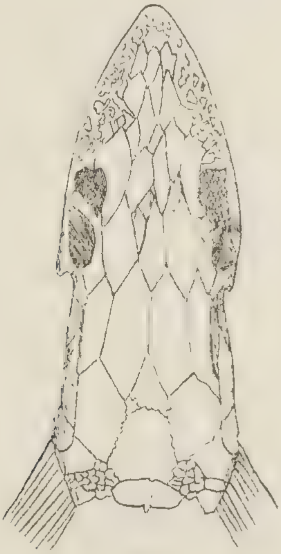


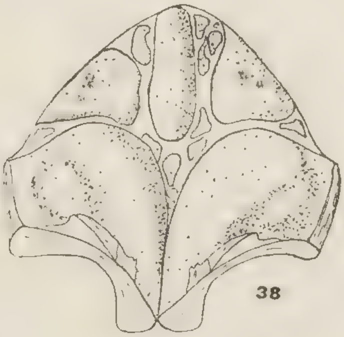
Fig. 36.—*Polyodon*. The dermal roofing bones (from Bridge, 1878).

The basal ossifications on the skull of *Acipenser* are similar to those of *Polyodon*. The synpterygoid is broader. There is a gap between the fore end of this bone and the posterior end of the flat "vomer" in front of it. This last is not continuous to the end of the snout but anteriorly is broken up into a closely fitting series of pairs of scutes. The roof pattern of *Acipenser* is so similar to that of *Scaphyrhynchus* that one illustration would serve for both. These two genera are as bewildering in the plurality of the dorsal scutes as *Polyodon* and *Psephurus* are in their paucity.

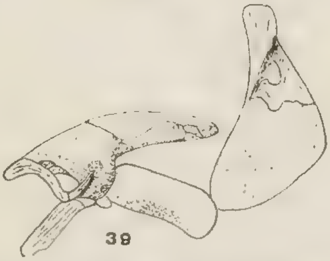
Gregory's interpretation of these bones is provisionally accepted and his illustration of *Scaphyrhynchus* is reproduced (Fig. 37).



37



38



39

Fig. 37.—*Scaphyrhynchus*. The dermal roofing bones (from Gregory, 1933).
Fig. 38.—*Acipenser*. The palate (from Parker, 1882).
Fig. 39.—*Acipenser*. The jaws and the suspensorium (from Parker, 1882).

There appears to be no way, as yet, to determine the actual homologies of the numerous scutes on the dorsum of this skull, and, indeed, it is even questionable whether they should not be regarded as evidence that the primitive bony fishes had no settled plan of fragmentation of the bony shield, or was it want of plan in the integration of numerous tiny ossicles? This latter is probably the most likely explanation.

The interpretation of the illustration, then, is accepted, provided the nomenclature is regarded as being purely topographical and not implying homologies.

The palate of the Sturgeons (Fig. 38) is an altogether curious structure. The palato-quadrate cartilages appear as though curved the wrong way, the concavity of the curve being outward instead of, as in all other elasmobranchs and bony fishes, on the inner side. The result is that the anterior ends do not meet in the usual symphysial union, but project forward side by side, and the medial edges of the two cartilages are in contact for a short distance, and then diverge caudad. So broad are the cartilages that they form a nearly complete cartilaginous palate behind the jaw and, swelling posteriorly, extend slightly behind the transverse level of the two Q-M. joints. Behind the "palato-quadrate palate" the roof of the mouth is added to by three large plates and a collection of small pellets of cartilage.

The actual margin of the jaws is supplied by a membrane bone developed independently of the palato-quadrate and by a lesser on each side, laterally, immediately in front of the jaw joint. Although the former touches and is applied to the anterior end and lateral edge posteriorly. Parker was probably correct in regarding these as not ectochondral in origin in either instance, but fairly certainly was he correct in the case of the anterior bone, which he designated the maxilla. Between the maxilla and the cartilage two, probably, ectochondral ossifications are found. These are both small and placed on the lateral surface, and encroach but slightly on to the dorsal surface. The more anterior of these was identified by Parker as the mesopterygoid (metapterygoid of this work), the other he termed the palatine (maxilla). The ventral, that is, the oral, surface of the palato-quadrate is largely covered by an ectochondral plate of bone which Parker identified as the pterygoid (palatine).

In *Polyodon* and *Psephurus* the palato-quadrate is essentially similar to that of the Selachii or Batoidei, and there is developed on its opposing and outer surface a single bone which has been designated the maxilla, and on its inner surface a bone which Traquair identified as the palatine. There is no trace of the curious palate of the Sturgeon.

The collection of palatal cartilages behind the palato-quadrate of the Sturgeon may be dismissed as being *sui generis* and without parallel elsewhere.

The maxilla in both chondrostean types may be regarded as the precursor of, and as completely homologous with, the maxilla in the tetrapods and the bony fishes, that is, with the bone which has, in the past, been so universally designated palatine in the latter fishes.

It is possible that in the Sturgeon we are permitted to observe this bone in the making, as it were. That which Parker designated the maxilla being only the dermal alveolar, tooth-bearing component, whilst the three ectochondral ossifications are the palatine lamina. Prior to the appearance of Landacre's confirmation of the work of Platt and Stone, one would have advanced in support of this suggestion the fact that the teeth are certainly ectodermal structures whilst the ectochondral bone is mesodermal. Even so, although we now know that the cartilage is certainly ectodermal, and its osteogenetic tissue possibly so, it is still possible to recognize in the tooth formation a later ectodermal invasion of the deeper tissues than that from the neural crest which gave rise to the cartilages, so that thus modified the argument still holds.

The lower jaw and its suspension in the Chondrostei (Figs. 39, 40) is essentially similar to that of the Plagiostome, resembling more particularly that of the batoid rather than the selachian forms.

The segmentation of the lower end of the hyomandibular cartilage to form a symplectic has been remarked upon as evidence of teleostean affinities. I know of no teleostean in which the hyomandibular cartilage is segmented. It is highly doubtful whether the so-called symplectic bone of the teleosts is comparable at all with the cartilage of the Chondrostei. The *cartilage* intervenes between the hyomandibular and the quadrate, completely separating the two, and it is formed by segmentation from the lower end of the former. The *bone* is developed in the lower end of the hyomandibular cartilage and here the resemblance ends. It lies behind the quadrate, and does not intervene between that and the hyomandibular.

On the other hand, there is no slightest trace, within the suspensorium of the Chondrostei, of that separation of the quadrate from the rest of the palato-quadrate bar, or of the presence of the metapterygoid process from which the shaft of the quadrate and the epipterygoid are developed. These are two absolutely constant features of the mandibular suspension in the Teleostei and, moreover, essentially characteristic of the whole of the bony fishes. These and the attachment of the palatal arch to the skull, anteriorly separating the two cartilages, are the outstanding features of the teleostean suspensorium and palatal arch.

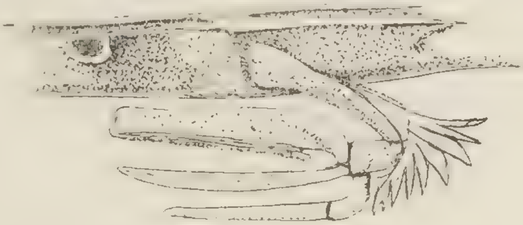


Fig. 40.—*Psephurus.*

Notwithstanding the absence of these essential features, Gregory writes (1933, p. 120), " the entire suspensorium (of the Chondrostei) is *evidently* a modified actinopteran type, differing from the elasmobranch(ian) especially in the presence of a large symplectic and of an ' opercular ' plate " (the italics are mine).

It were foolish to deny Professor Gregory the use of the personal factor in evaluating these features, but one may be permitted to comment that, at least, the evidence is not obvious. It seems that it would be a good deal nearer the truth to say that it is " evidently a slightly modified elasmobranchian suspension ".

It may be said of the skull of the Chondrostei, (1) that whilst it possesses outstanding elasmobranchian features it does not possess one single teleostean feature that is not also possessed by the Holocephali, except the ectochondral bones, and (2) that it differs from the skull of every known bony fish in the complete absence of endochondral ossifications.

Gregory's view of the Chrondostei is that they owe their characteristics to " degenerative specialisations from an actinopteran starting point " (1933, p. 120). This view, however, is based entirely on his interpretation of the special features of the group and is not supported by the citation of any definitely actinopteran characters. He asserts that the " shoulder girdle (of *Polyodon*) is that of an actinopteran, not that of a progressive shark ".

After dissecting that of *Acipenser* and comparing it with that of several selachian and batoid forms I am able to agree with this dictum. Stripped of its derm bones the cartilaginous girdle is most emphatically essentially similar to that of the Elasmobranchs and unlike that of the Actinopterans.

I do not suggest that the Chondrostei should be regarded as progressive sharks. To me they appear to be descendants of a primitive elasmobranchian branch which had been " cut off " with a very small share of that osteogenetic potential which was in fuller measure the heritage of those other branches which yielded the whole of the bony fishes and animals.

Gregory's suggestion that they are derived from an actinopteran starting-point implies an almost complete reversal of evolutionary forces and a return to primitive elasmobranchian conditions.

One striking difference there is between the cartilaginous structures of the chondrostean skull and that of the elasmobranchian fishes. This is that in the Elasmobranchii all the cartilage is either covered or permeated by exceedingly tough fibrous tissue, whilst there is no such covering or permeation in the chondrostean skull. Herein the Chondrostei resemble not only the Teleostei, but also those primitive amphibia, the Dipnoi.

It would almost seem that the acquisition of osteogenetic power was at the expense of this tough perichondrium.

This suggests the following further speculation. The Chondrostei, deficient in osteogenetic power, were unable to develop solid endochondral replacements, or ectochondral covering plates, in or on the cranial walls, and had also lost the power to encase the skull in that tough fibrous investment which not only strengthened them but also made of them fit " fixed " and rigid points for the origin of muscles.

With more or less futility, an attempt was made to compensate for the absence of rigidity by the utilization of the dermal tubercles. These were aggregated into scutes of varying sizes and articulated together in the production of a complete cephalic shield and dorsal and lateral body series.

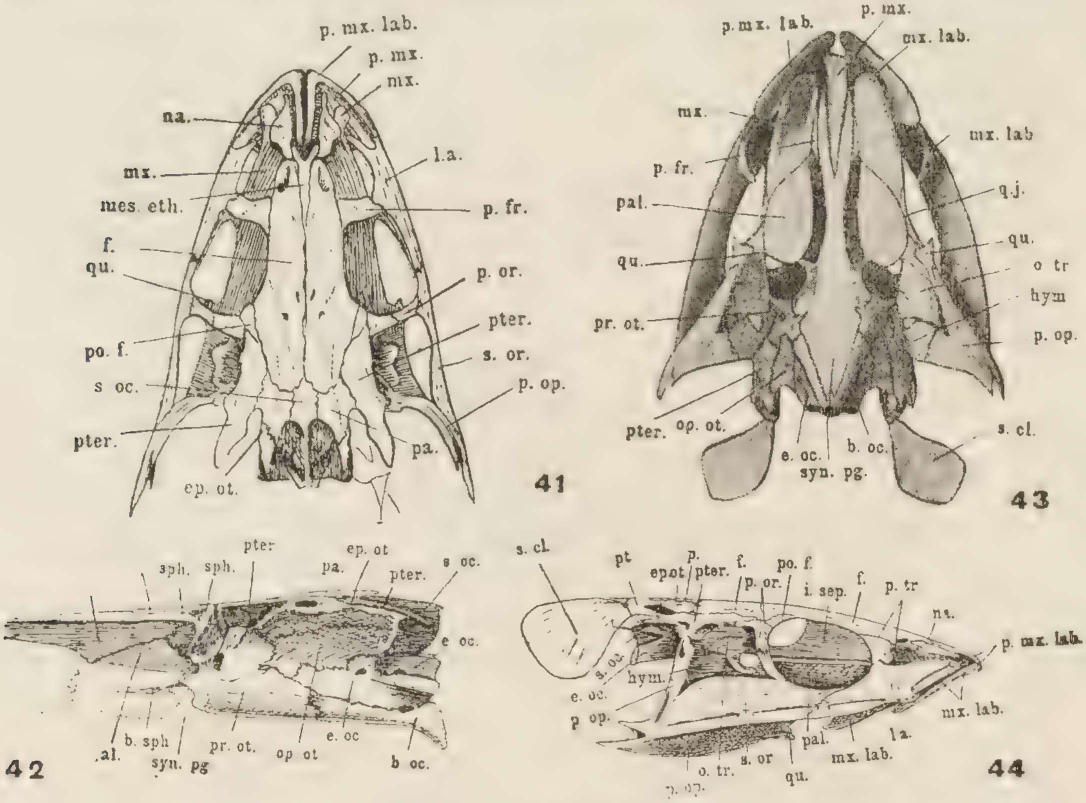
This is, of course, pure speculation and is only intended to point out that the Sturgeons may be regarded as illustrating one of nature's failures—an ineffectual attempt to obtain that cephalic and bodily rigidity with flexibility which was essential to the development of a mechanism capable of directionally purposive rapid movement, and to obtain it without the solid, and yet flexible, endoskeleton.

The " operculum " of *Psephurus* is fitted very neatly to the lower half of the hyomandibular ; in the Sturgeon it is fitted to the hyomandibular for a greater length.

This relation suggests that it is really a preoperculum. Gregory states (p. 426) that it " has no contact with the hyomandibular " and regards it as a suboperculum. This observation and identification probably results from the study of mounted or disarticulated material and the neglect of the material in the flesh and of dissecting instruments.

THE SKULLS OF THE BONY FISHES.

In this, as in other sections describing the skulls, no claim is made to have dealt with the subject exhaustively. The aim has been to describe one or two skulls which may be regarded as typical of each group, with a view to providing a standard of reference for subsequent discussion.


p. mx. lab.
p. mx.
mx.
na.
l.a.
mx.
mes. eth.
p. fr.
f.
qu.
p. or.
pter.
po. f.
s. or.
s oc.
p. op.
pter.
pa.
ep. ot.
41
p. mx.
p. mx. lab.
mx. lab.
mx.
mx. lab
p. fr.
pal.
q.j.
qu.
qu.
o tr
hym
pr. ot.
p. op.
pter.
op. ot.
s. cl.
e. oc.
b. oc.
syn. pg.
43
pter
sph.
sph.
ep. ot
pa.
pter.
s oc.
e oc.
b. sph
al.
syn. pg
pr. ot.
op ot
e. oc
b oc.
42
s. cl.
pt
p.
epot
pter.
f.
p. or.
po. f.
i. sep.
f.
p. tr
na.
p. mx. lab.
s. oc
hym.
e. oc.
p op.
mx. lab.
pal.
la.
mx. lab.
s. or
o. tr.
qu.
p. op.
44

Figs. 41-44.—*Platycephalus.*

The examples chosen here are *Platycephalus* and *Paradicichthys.* Of the former I give only the illustrations which accompanied my detailed description published in 1926. Throughout the description of *Paradicichthys* free use has been made of the terminology which I proposed (1926), in an attempt to provide a standardized nomenclature for ichthyo-craniological descriptions, and in the discussion on the maxillo-ethmoid articulation in the skulls of bony fishes, which appeared at the same time.

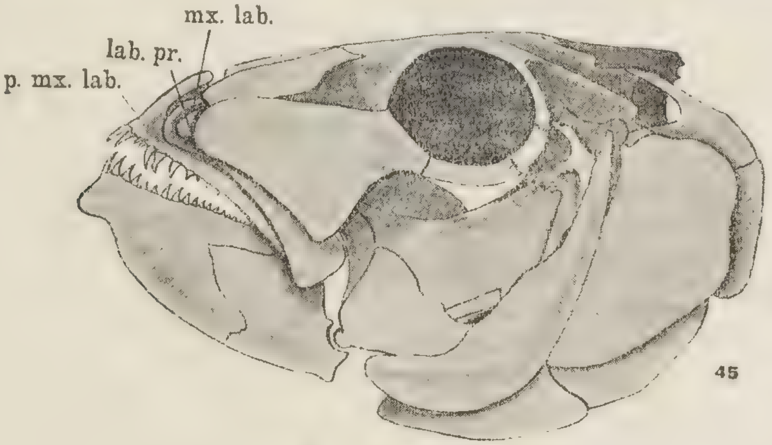
Paradicichthys venenatus Whitley.

(Figs. 45-56.)

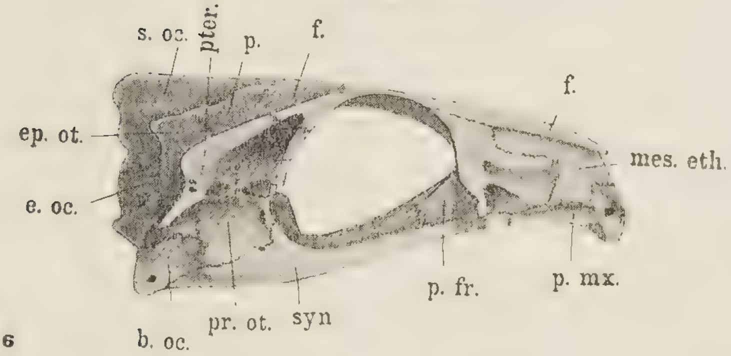
The general contours of the skull and its regions will be readily gathered from the drawings.

The dilator fossa is exceptionally large, and extends medially under a large portion of the floor of the temporal fossa. The anterior and upper part of this fossa lies between two laminae of the frontal bone. The lower of the laminae in question sutures with the upper margin of the sphenotic, the upper lamina with the upper margin of the pterotic bone, which latter is thrown right across the sphenotic bone to reach the lamina of the frontal. The floor of the fossa is formed, for the most part, by the outer portion of the upper surface of the body of the sphenotic bone and to a lesser extent by an undercurved part of the pterotic bone which sutures with the sphenotic as it crosses it. This suture is interrupted on both sides of the skull by a foramen, but the foramen on the right side is much larger than that on the left. The foramina probably transmit blood vessels. The roof slopes from the floor upward and forward to the top of the anterior wall; for the most part it is formed by the pterotic bone.

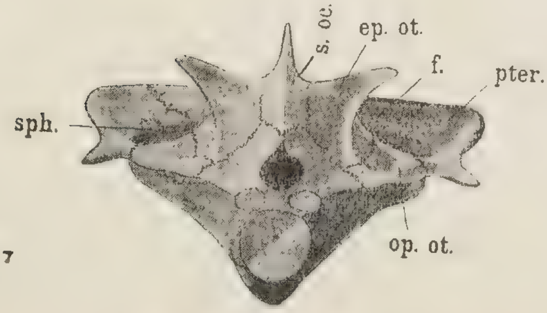
The temporal fossa is also larger than is usual; it is devoid of a roof but, for the rest, well defined. The median wall, slightly overhanging, is formed by the epiotic process behind and an



45



46



47

Figs. 45-47.—*Paradicichthys.*

upstanding flange of the parietal and frontal in front. Posteriorly the floor is defined from the sloping outer wall by a very definite sulcus where the pterotic turns under to suture with the sphenotic bone, and behind this sulcus by an angle along which runs the suture between pterotic and opisthotic bones. In front of the sulcus the fossa is much shallower, and the sloping outer wall meets the bottom of the inner wall at a wide angle, and has become the floor. In front of the pterotic process the outer boundary of the fossa is clearly indicated by the change in the character of the surface of the frontal bone ; beyond the fossa this bone is subdermal and presents the usual roughened surface of subdermal bones. Medial to the pterotic process, the floor of the fossa is formed by the sphenotic and opisthotic bones. The posterior margin of the fossa is a curved ridge which begins above to the inner side as the posterior margin of the epiotic process, prominent and outstanding ; this merges below into a ridge of low relief which turns ourward and then slightly upward again, to reach the posterior end of the outer wall at the root of the pterotic spur. Above this curved margin the fossa is crossed from within out by a prominent rounded ridge which throws the floor behind it almost into the vertical plane. This ridge commences below the epiotic process just in front of its hinder margin and, crossing the body of the epiotic and opisthotic bone, terminates at the root of the pterotic spur. The posterior semicircular canal lies immediately beneath the upper end of the ridge, and was doubtless responsible for its formation.

The occipital fossa is bounded laterally by the inner wall of the temporal fossa. The anterior portion of the floor is nearly in the horizontal plane, whilst the posterior portion is nearly in the vertical ; the angle between these two portions is a ridge which runs across the floor from the epiotic process. The median wall is, of course, the occipital crest and its forward continuation. This wall stands out behind the vertical portion of the floor and is supplemented below by the sloping superior vertical lamina of the exoccipital bone. The floor of the occipital fossa is carried out laterally below the inferior limit of the temporal fossa, and is itself limited below by the buttress of the exoccipital bone.

The large size of the hollow ethmoid bones gives to the preorbital region a deceptive appearance of solidity. The single facet for the maxilla is placed far forward on the anterior end of the prefrontal below and lateral to the nasal cavity. The frontal bones overlie the greater part of the mesethmoid ; only a small vertical portion of that bone is to be seen in front of them. The large nasal bones are firmly bound to the lateral edges of the frontal bones in front of the prefrontals, and also to the upper edges of the first subocular bones, to enclose the greater part of the nasal capsules in bony walls. The nasal apertures lie close together behind the posterior margin of the nasal bone and in front of the prefrontal. In this region the outer wall of the capsule is membranous, filling in a triangular gap between the two bones mentioned and the hinder half of the upper border of the first subocular ; for the rest, the whole of the capsules are enclosed by bony walls.

The trigemino-facialis chamber has the incomplete outer wall formed by a bridge of bone developed from the prootic ; a little square of the same bone thrown up from below forms an incomplete front wall to the chamber.

Bones of the Cranium.

The *basioccipital* bone presents all the usual parts but it is modified in such a way as to disguise that fact to some extent. The myodomial recess is very large and is completely roofed. The saccular recesses are placed at and above the level of the myodomial roof (" hypomyodomial skull "). Between these two recesses there is a solid, roughly cubical shaped, mass of bone, which, besides forming the inner walls of the saccular recesses, also forms the roof of the myodome and the occipital segment of the cranial floor. The cube is excavated behind by the large azygos sinus, which extends right across the width of the floor. Behind the azygos sinus the basioccipital bone is covered by the two exoccipital bones. This suture between basi- and exoccipital bones swings forward, round the edge of the sinus and along the sides of the occipital segment of the cranial floor, and at the same time along the middle of the length of the roof of the saccular fossa of each side. The basioccipital element in this suture is a narrow flange which stands out from the side of the top of the cubical mass described above. These little flanges, together with the flat top of the cubical mass, replace the horizontal laminae of the exoccipital bones which, in many fish skulls, form the occipital segment of the cranial floor in front of the sinus ; and it may be said that the flanges suture with the exoccipital bones along the line of origin of the replaced laminae. The basal lamina of the basioccipital is very thick and somewhat narrow ; it is incised along the centre of its width toward the hinder end by a deep narrow groove which perforates the entire thickness of the bone just in front of the condylar edge. Only portion of this perforation of the myodomial floor is closed by the hinder end of the synpterygoid bone. Though the saccular recesses are placed at a higher level than the myodome, they do not bulge beyond it laterally, so that there is no trace of a saccular bulla, and the vertical lamina of the bone is without prominences above the myodomial swelling. The fore end of the cubical mass sutures with the hinder ends of the horizontal laminae of the prootic bones. Immediately to the outer side of this contact there is, in the dried specimen, an oval foramen of some size which leads from the saccular cavities on each side to the myodome ; below this foramen the vertical lamina of the basioccipital bone sutures with the myodomial lamina of the prootic ; above and to the outer side of the foramen the suture between the basioccipital and prootic bones crosses the floor of the saccular recess. At the outer end of this last suture the vertical lamina of the basioccipital sutures with the inferior margin of the inferior vertical lamina of the exoccipital bone. There is an oval foramen on both sides of the azygos sinus which leads into the hinder end of the saccular cavity of its side (*vide* Figs. 51A, B).

The *exoccipital* is a much more normal bone than the basioccipital. No part of the superior vertical lamina is actually in the vertical plane, but each slopes towards its fellow, to meet above the foramen magnum. The buttress is well developed, and is continued out by a ridge, developed behind the posterior end of the horizontal semi-circular canal, to meet the prominent posterior edge of the opisthotic bone. The inferior vertical lamina is a little less extensive than usual. The external aperture of the occipito-spinalis foramen is found above, and that of the vago-glossopharyngeal canal below, the buttress. The horizontal lamina is confined to the region of the cranial floor behind the azygos sinus. The internal aperture of the occipito-spinalis canal is situated just above the azygos sinus, and that of the vago-glossopharyngeal canal at the extreme anterior edge of the postotic cranial wall, where it overhangs the posterior ampullary cavity. As is usual the otic mass of the bone lodges the posterior ampullary cavity with the contiguous portions of the posterior and horizontal canals ; it also forms the roof and side wall of the saccular cavity, and this also is usual.

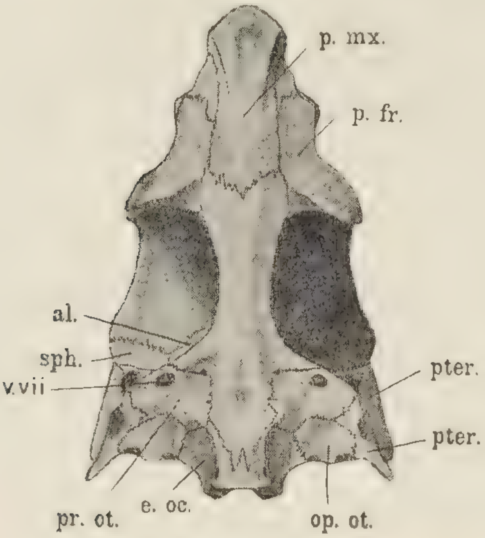
The *supraoccipital* bone presents little of special interest ; the vertical lamina is much reduced, the crest well developed, but not large.

The general shape of the *epiotic* bone will be gathered from the drawings ; the bone forms the postero-superior corner of the otocrane and lodges the greater part of the posterior semi-circular canal. The surface of articulation of the upper arm of the post-temporal, on the dorsum of the epiotic process, is large and smooth.

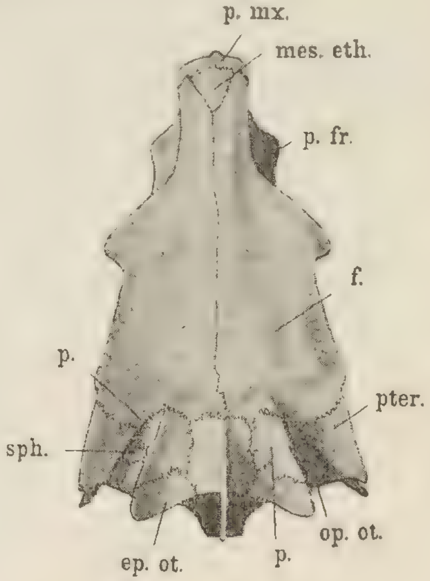
The *pterotic* bone takes no part in bounding any of the otocranial recesses or canals ; it is a flattened bone which is sutured by its inferior margin to the juxtaposed edges of the opisthotic and prootic bones and to the dorsum of the sphenotic, crossing this last bone to be sutured to the upper of the two lamina into which the hinder end of the frontal splits. Posteriorly this flattened bone stands nearly vertically ; where its anterior margin sutures with the frontal the bone is oriented more nearly in the horizontal plane. The postero-inferior corner of the bone, just above the suture with the opisthotic, is produced into a well developed " spur ". The posterior hyomandibular articular facet is borne on the under side of the bone immediately in front of the root of the spur. The postero-superior corner of the bone is slightly swollen and gives attachment to a band of fibrous tissue which replaces the supratemporal bone.

The irregularly shaped *opisthotic* is wedged in between the pterotic and prootic in front and to the outer side, the epiotic and exoccipital behind and to the inner side, and the sphenotic in front. The bone lodges portion of the horizontal semi-circular canal and at its postero-lateral corner bears the facet for the articulation of the inferior arm of the post-temporal.

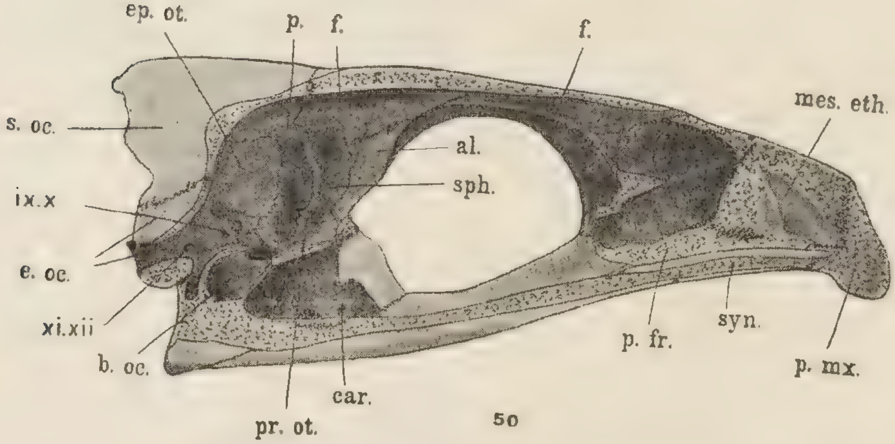
The body of the *prootic* bone is relatively small, the myodomial lamina relatively extensive. The former is oriented mainly in the horizontal plane, the latter mainly in the vertical, so that a proper idea of its conformation can only be gathered by the study of both Figures 47 and 49. The extent of the body of the bone showing on the posterior orbital wall is rather greater than is usual ; the angle between these two faces of the body is accentuated by the bridge of bone which forms the outer wall of the trigemino-facialis chamber. The bone takes a lesser share than is common in the formation of the anterior hyomandibular facet. Little of the myodomial lamina is covered by the synpterygoid. The horizontal lamina is sharply differentiated into cranial-floor and saccular-floor components. That portion of the lamina which forms the prootic segment of the cranial floor is triangular in outline, the base of the triangle being at the mid-line, the apex at the trigemino-facialis fossa. At the hinder margin of this segment the lamina dips vertically a little way and then slopes down, back and laterally, forming the oblique anterior wall and part of the floor of the saccular cavity. The lamina between the lower part of the arcuate and the trigemino-facialis fossae is well developed, and the large anterior aperture of the horizontal bony canal is placed immediately to the outer side of, and behind, the former fossa. The carotid canal interrupts the suture between the prootic and the latter bone.



48



49



50

Figs. 48, 49.—*Paradicichthys.*
Fig. 50.—*Paradicichthys.* Median section of the neurocranium.

The *sphenotic* bone bears a rather larger post-orbital lamina than is usual, and at the inferior margin of this lamina the bone bears the greater part of the anterior hyomandibular articular facet. The body is of quite irregular shape; it appears in the inside of the skull, where it constitutes the upper half of the arcuate fossa and the intracranial temporal fossa.

The *alisphenoid* is a flexed lamina of bone which sutures with the alisphenoid process of the frontal, the sphenotic, prootic, and basisphenoid bones. There is no pterygoid process and no contact with the synpterygoid.

The transverse arm of the basisphenoid is almost in the vertical plane; it sutures with the alisphenoid and with the prootic to the inner side of the trigemino-facialis fossa. The vertical arm is broader and thinner above than it is below where it sutures with synpterygoid.

The *parietal* bone presents a small oval area in the roof of the cranial cavity; externally, it is much more extensive. Of irregular outline, it is placed between the supraoccipital, epiotic, sphenotic, and frontal bones. It is crossed by a prominent ridge which is thin and plate-like in front, where it sutures with a similar process of the frontal, but behind it becomes much stouter and forms a very strong buttress to the epiotic process.

The shape of the *frontal* bone will be gathered from the drawings. Posteriorly the bone is bilaminate on both sides of the little upstanding plate which sutures with the parietal ridge. To the inner side of this line the upper lamina is the cranial roof, the lower lamina, the alisphenoid process; to the outer side of the line the upper lamina is the roof of the dilator fossa, the lower (much shorter) sutures with the superior margin of the postorbital plate of the sphenotic.

The *synpterygoid* is rather broader than in other comparable skulls; it is continued back along the basioccipital almost to the condylar edge, leaving a basi-myodomial foramen between its bifurcated posterior end. There is no alisphenoidal process.

The drawings must again be consulted to gain an idea of the shape of the *prefrontal* bone. The preorbital process is massive and bears no facet for the articulation of the maxilla. There is a knob on the infero-lateral corner, to which the first subocular is firmly bound but not articulated. The situation of the preethmoid maxillary articular facet is quite peculiar. In the great majority of the acanthopterygian fishes this facet is found on the under side of the preorbital process just where it joins the body of the bone. In this form it is divorced from the preorbital process altogether; the body is inordinately prolonged forward and the facet is placed on the extreme anterior edge thereof. The postero-ventral process is a massive corner which sutures with a process of the synpterygoid developed to accommodate it. The postero-dorsal process is poorly developed.

The *mesethmoid* is a larger bone than usual; for the most part covered by the frontal bones, it shows a small subdermal area between their divergent forward ends. The median ridge so characteristic of the bone is present, but is very short and is very nearly vertical.

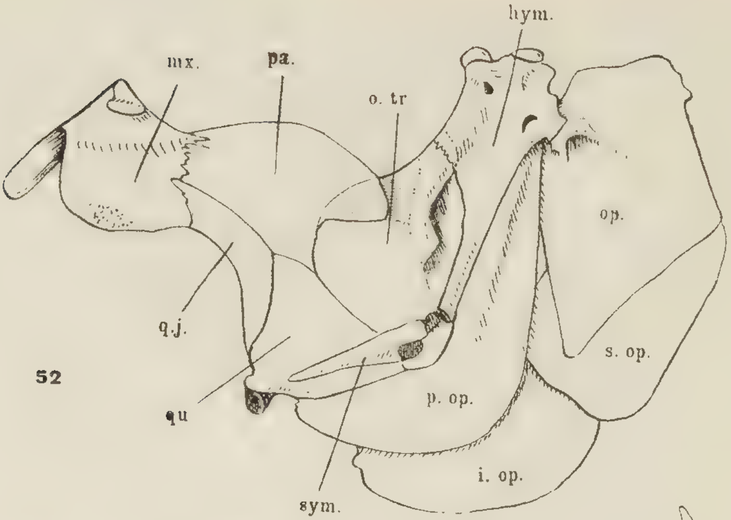
Both these two last bones are constructed of very open-meshed cancellous bone and are further excavated by large cavities filled with loose fatty tissue. No definite cartilage was found between them.

The steep ascending process of the *premaxilla* is flush with the forward end of the mesethmoid. There are two or three rows of small teeth similar to those on the premaxillary labial on the alveolar border. The comparatively broad palatine plate is rather abruptly truncated posteriorly.

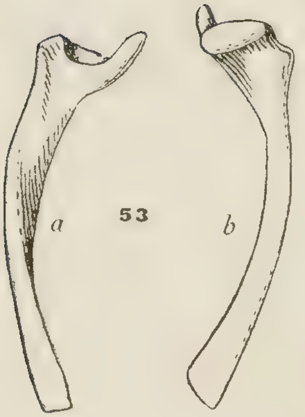
Bones of the Upper Jaw and Palate.

(Figs. 52-56.)

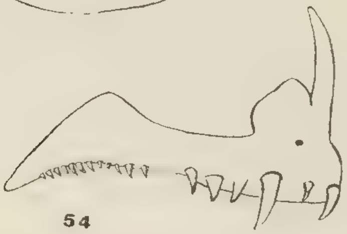
The *hyomandibular* bone may be described as presenting a body and an elongated ventral process. The body is roughly square in outline, the lower side being produced out into the process. The bone is binarticulate; the anterior condyle stands up and forward from the antero-superior corner of the body, the posterior condyle is placed on the dorsal edge of the bone, nearer the posterior than the anterior corner. The upper opening of the canal for the hyomandibular branch of the facial nerve is just behind and below the anterior articular facet, the lower opening is on the posterior edge of the process about the centre of its length. The former is, of course, on the inside of the bone, the latter is outside the strong fibrous tissue that binds the process to the preoperculum. The well developed facet for articulation with the operculum is on the posterior edge of the bone a little below the centre of the body. A stout ridge crosses the body of the bone on the outside from the anterior articular facet to the base of the opercular facet. In front, this ridge takes the form of a rounded buttress to the articular head, further back it becomes higher and sharper, and the free anterior edge of this higher part stands forward over the buttress-like portion. *In situ*, this projecting point nearly touches, and is bound to, the outer corner of the post-orbital plate of the sphenotic. At its hinder end the ridge becomes merged with the prominent upper end of the inferior process of the bone. From the angle where these meet, there arises a low ridge which extends diagonally down and forward across the body of the bone to the antero-inferior corner of the body; just before the inferior margin of the body is reached, this low ridge is undercut so that the extreme corner of the body is bilaminate. The


hym.
mx.
pa.
o. tr
op.
q.j.
s. op.
qu
p. op.
i. op.
sym.

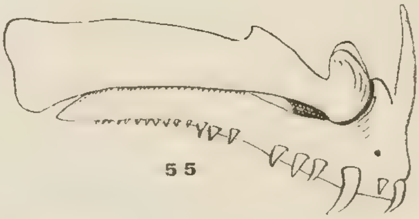
52



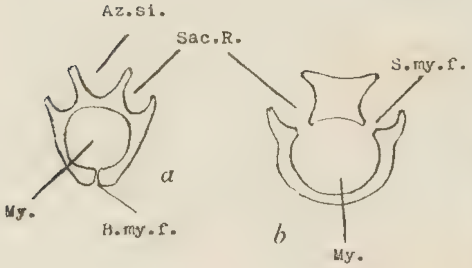
53



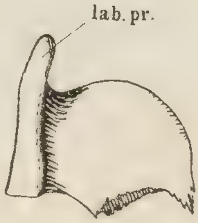
54



55


Az.si.
Sac.R.
S.my.f.
a
My.
B.my.f.
b
My.

51



56

Fig. 51.—*Paradicichthys*. Transverse sections through the basioccipital bone. A. is the more posterior of the two. Az.si., Azygos sinus ; B.my.f., Basimyodomial fenestra My., Myodome ; Sac.r., Saccular recess ; S.my.f., Sacculomyodomial foramen.

Fig. 52.—*Paradicichthys*. The palatal arch and the suspensorium.

Fig. 53.—*Paradicichthys*. The maxillary labial bone.

Fig. 54.—*Paradicichthys*. The premaxillary labial bone.

Fig. 55.—*Paradicichthys*. The two labial bones.

Fig. 56.—*Paradicichthys*. The maxilla.

outer lamina is thin and sutures with the outer lamina of the top corner of the metapterygoid ; the inner lamina, much thicker, sutures with the stout inner lamina of the same bone. Between the two bones there is a narrow passage, and through the passage there passes, in the flesh, a strong tendon of the levator arcus palatini muscle which will be referred to again later. When the bones are in place it is found that the upper surface of transverse ridge is in the plane of, and continues backward and down, the floor of the dilatator fossa, and that this floor is complete but for an oval foramen just behind the orbit. The boundaries of this foramen are : the outer corner of the postorbital plate of the sphenotic in front, the buttress of the anterior articular head of the hyomandibular to the inner side, the shelf-like process of the same bone behind, and the anteriorly projecting point of that process on the outer side. Another tendon of the levator arcus palatini muscle passes through this foramen, and it also will be referred to again later.

The shape of the metapterygoid will be gathered from the drawings (Fig. 52, *o.tr.*) ; except at the dorsal corner it is a thin lamina of bone ; at that corner it is bilaminate and the inner lamina is thickened. The extent of this bilamination has been indicated on the drawing by dotted lines ; the whole of the inner surface of the outer lamina covered by the inner, and between it and the inferior, process of the hyomandibular, and also a small triangular area below the inner lamina and in front of the same process, gives attachment to those fibres of the levator palatini muscle which insert on the tendon that has been described as passing down between the two laminae of the bones.

The *symplectic, quadrate, ectopterygoid* and *palatine* bones need no description ; their shape is sufficiently shown in the drawings.

The *maxilla* is acrartete. The body of the bone is a plate which is much thickened towards the medial border. The outer thinner portion of the bone sutures flush with both sides of the fore end of the ectopterygoid ; the thickened medial portion sutures along its posterior edge flush with the under surface of the fore end of the palatine, but presents a rough surface above the level of the upper surface of that bone, this roughened surface being attached by tough fibrous tissue to the under surface of the preorbital process of the prefrontal bone. The dorso-median and anterior border bears a solid bar of bone which is continued forward as the labial process and carries the articular facet on its truncated posterior end. There is a limited tooth-bearing area on the outer margin of the thinner portion of the bone. The teeth are little pegs, similar to those on the premaxilla, but smaller.

The form of the opercular bones is sufficiently shown in the drawings.

THE PERIOCULAR BONES.

There are four of these bones present. The outline of the first is clearly shown in the drawing ; where it is attached to the prefrontal bone it is thickened and bears an articular facet. The second extends the full length of the under side of the orbit ; it is attached to the inner side of the first almost as far forward as the attachment of that to the prefrontal. This second subocular bears a subocular shelf along its full length. There are two short postoculars, the upper of which is attached to the frontal just where that bone becomes bilaminate, behind and above the orbit.

THE CRANIAL BOUNDARIES, THE OTOCRANE AND THE MYODOME.

The occipital segment of the cranial floor is formed by the horizontal laminae of the exoccipital bones behind the azygos sinus, and by the basioccipital in front of that sinus. The azygos sinus is particularly large ; it extends across the full width, and along nearly half the length of the occipital segment of the floor. A large foramen on both sides places it in communication with the two saccular cavities. In the mesotic region there is a deficiency on each side in the roof of the saccular cavities, but since the lateral cranial obturator membrane rises vertically medial to these deficiencies, there is no basicranial obturator membrane ; the fore end of the upper surface of the basioccipital bone sutures with the hinder ends of the horizontal laminae of the prootic bones. Immediately forward of this suture the mesotic section of the floor widens rapidly. The pituitary fenestra is a narrow transverse slit, and is followed by a narrow prepituitary bridge which is tilted almost into the vertical plane.

The lateral cranial obturator membrane is attached above in front to the top of the lamina which separates arcuate from temporal fossa ; from here the line of attachment is continued down the free border of that lamina and along the hinder edge of the mesotic section of the floor. It now turns back along the inner (median) side of the gap in the roof of the saccular cavity, then laterally along the hinder margin of that gap. In this situation it is attached to the free anterior margin of the flange developed along the side of the cubical mass of the basioccipital bone. Leaving this structure, it reaches the free anterior margin of the postotic section of the cranial wall. This free margin terminates just above the posterior ampullary cavity, and from this point the line of attachment turns medially and up and becomes lost in the mass of loose connective tissue which fills the top of the cranial cavity above the level of the exoccipito-supraoccipital suture. Thick behind, this mass thins as it reaches forward, leaving the roof of the temporal fossa free of aught but a layer of fibrous tissue.

The lateral cranial obturator membrane is quite well defined as usual, in close proximity to the various bony laminae to which it is attached, but, removed from those laminae, it is even more indefinite than usual, and it is almost impossible to delimit the fatty tissue filling the temporal fossa and that, less fatty, tissue in which the membranous labyrinth is packed.

The temporal fossa is large and the extensive alisphenoid bone makes a more complete front wall than is usual. The spheno-obturator membrane is narrow, but broadens below just above the prepituitary bridge.

There are three perforations in the depth of the well-formed trigemino-facialis fossa; of these the two lower ones open directly into the little trigemino-facialis chamber, and the third just to the inner side thereof. The oculo-motorius foramen is placed to the inner side of the fossa, almost within it, and opens directly forward. The foramen of the sixth nerve perforates the mesotic floor directly in front of the saccular cavity and transmits the nerve to the myodome. No foramen for nerve IV is discoverable; it probably leaves the cranial cavity through the spheno-obturator membrane beside the optic nerve. It may be that that which is described above as the oculo-motorius foramen transmits a branch of the trigemino-facialis complex, in which case the third nerve must leave the cavity through the sphenotic fissure (Kesteven, 1918).

The myodome is particularly large, and its roof more complete than usual. There is no median deficiency, but two large oval foramina near the middle of the length of the roof lead into the saccular cavities. There is a median basimyodomial foramen at the extreme posterior end of the floor, and a rather large carotid foramen perforates the side wall far forward and low down, interrupting the suture between the ascending process of the synpterygoid and the myodomial lamina of the prootic.

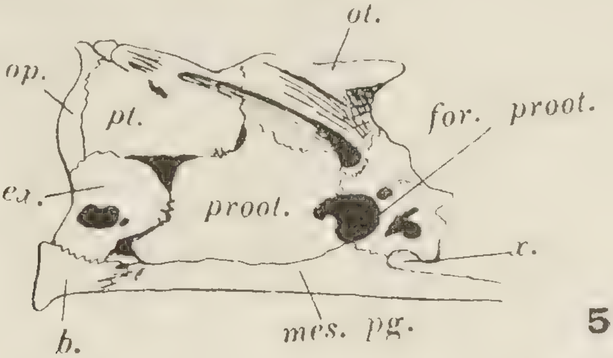
Paradicichthys and *Platycephalus* are two fairly typical examples of the modern teleosts and they may be accepted as fairly exemplary of the Acanthopterygii. Within this large group of the fishes there are many variations in skull form, but such variations affect the relative development of the component bones, so that they may be regarded as alterations of degree rather than of kind. In others of the many groups of the modern bony fishes the variations may be said to be of kind as well as of degree. W. K. Gregory (1933) has recently presented us with brief disjointed descriptions but excellent illustrations of a very large number of these variations in the arrangement and relative development of the bones. Numerous and extensive though these variations be, it is still, in the Teleostei, possible in all instances to regard every skull examined as presenting a variation of the central acanthopterygian type described above, rather than a new type. It were impossible to review all these variations and would serve no good purpose here, but a few of the more important may briefly be referred to.

In general, the median edge of the palatal arch is free from the base of the skull, and the arch of the palate between the two is completed by the "palatine fascia". In certain forms, e.g. *Arapaina*, *Notopterus*, *Gymnarchus*, *Mormyrops* and *Gnathonemus*, on the other hand, the median edges of the palatal arch bones are firmly ankylosed to the synpterygoid along the base of the skull.

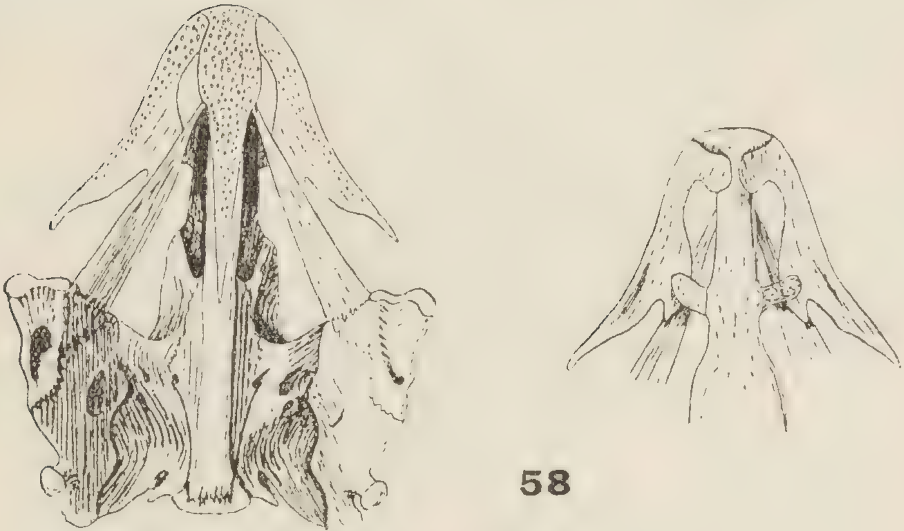
The number of otic bones is variable; the full complement of five is present in both the examples described: the opisthotic and sphenotic are the two most commonly absent. The basisphenoid is another bone which may not be present. The myodomial chamber is not developed in quite a number of fishes, e.g. *Tandanus* (Fig. 57). The labial bones are subject to wide variation in size and shape, and in some fishes are absent altogether, e.g. the Eels (Fig. 58). These last two also exemplify two of the many variations in the shape of the maxilla.

The development of some of the bones in the fish skull will be discussed later; at this juncture it may be mentioned that the amount of the chondrocranium remaining, encased in the bones in the adult cranium, is subject to variation. In general it may be stated that those fish among the Teleostei which, by common consent, are regarded as the most primitive, retain more cartilage than do the more modern forms. In this respect the Malacopterygii closely resemble *Amia*, the most modern, in form, of the Ganoids, and present various stages between the almost entirely bony cranium of the Acanthopterygii and this largely cartilaginous cranium.

The recent ganoid skulls must be described.



57



58

Fig. 57.—*Tandanus.*
Fig. 58.—*Anguilla.*

Amia.

(Figs. 59, 60D, 61, 62.)

The nearly complete cartilaginous cranium recalls that of the Elasmobranchs, but differs in important respects. The cavum cranii is not continued from end to end at the same level. At the anterior boundary of the otocrane the cranial floor is lifted dorsad away from the base-line of the skull. There is a very large lateral cranial fontanelle exposing much of the structure of the otocrane. Except in the Holocephali, this is a feature not found in elasmobranchian crania. A large myodomial chamber is present below the anterior end of the cavum cranii; it is the presence of this cavity, never found in elasmobranchian skulls, which lifts the cranial floor away from the base-line. In front of the myodome, at the orbit, the cranium is laterally compressed as it is in the Teleostei. Beyond this the sphenoidal cavity is continued forward dorsally to a short distance anterior to the orbit. The two olfactory passages open from its anterior end, separated by a relatively thick cartilaginous partition. There are no olfactory capsules, in the elasmobranch sense; the passages open into comparatively small pits situated on either side of the base of a solid short rostral anterior end of the cranium. Behind the base of this rostrum and in front of the orbit, the cartilaginous axis of the cranium is laterally expanded, and the olfactory pits lie on the upper surface of this expansion near its anterior edge. There is here another point of difference from the elasmobranchian condition. In those skulls, excepting the Holocephali and Chondrostei, the nasal capsules are formed by relatively thin expansions of the anterior end of the cranium which form well nigh complete roof, and medial and lateral walls,

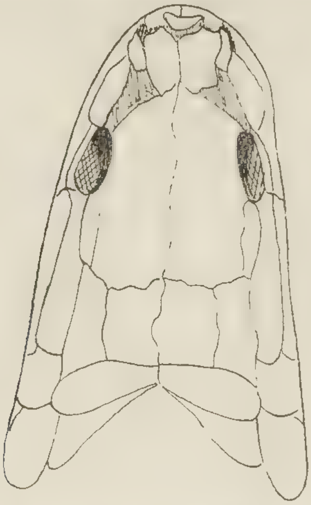
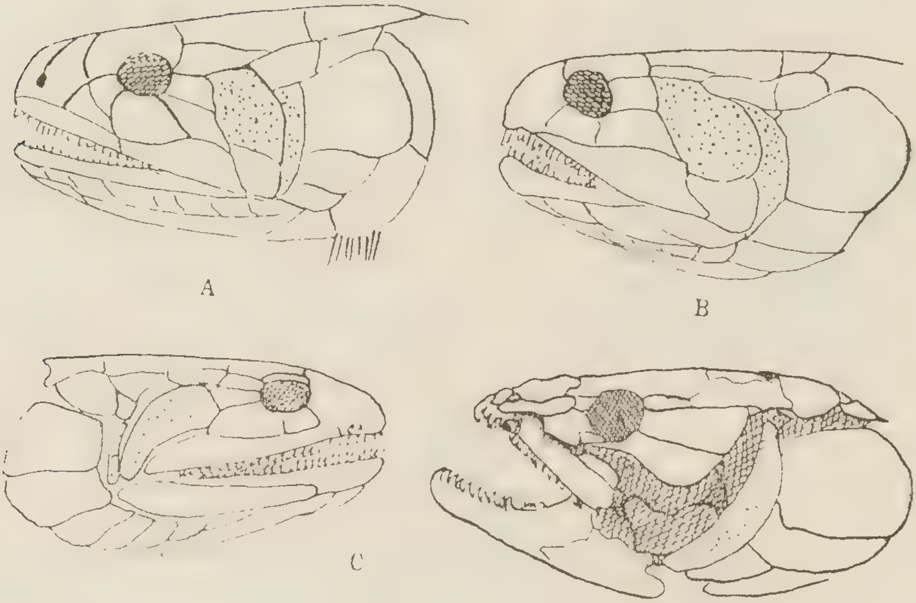


Fig. 59.—*Amia* (from Gregory, 1933).



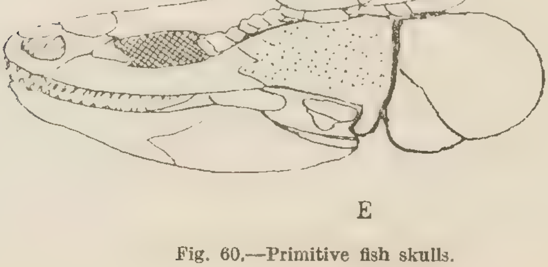


Fig. 60.—Primitive fish skulls.

floor and anterior wall being but poorly developed. Here we have a massive continuation of the cranial axis which provides a very complete floor and leaves all the other boundaries incomplete.

Of otic bones, three only have been recognized in the past; that which Allis designates the petrosal is, without doubt, the prootic; opisthotic and epiotic are also present. The number, size, shape, and relations of the other endochondral bones can be gathered from the figures.

In addition to the usual dorsal roofing bones, *Amia* possesses (1) a pair of scutes covering the epiotic, which have been named "tabulars" and "extrascapulars"; (2) a pair of "post temporal" scutes behind these and a relatively large pair of scutes between the post-frontals and the tabulars and lateral to the parietals—these have been designated squamosals by most writers in the past; Gregory terms them "pterotis" bones. This identification may be provisionally accepted.

The maxillo-palatine arch contains the usual number of bones found in the Teleostei, maxilla, palatine, ectopalatine, metapterygoid, symplectic, hyomandibular and quadrate.

There are three pairs of ossifications related to the anterior end of the ethmoid cartilage. One of these is a pair of small bones definitely developed on the cartilage on either side of the base of the short rostrum. These, Allis terms septomaxillaries. It is extremely doubtful whether they are really homologous with the similarly-named bone in the Amphibian skull, and the question appears not to be subject to satisfactory proof either for or against the identification.

The second pair is developed on the under side of the cartilage; they suture with the anterior end of the synpterygoid on either side of the mid-line and project slightly beyond the cartilage in the adult. Comparison with the prevomer in any or all lower Tetrapoda reveals no feature wherein they differ to an extent which would indicate that they are not homologous.

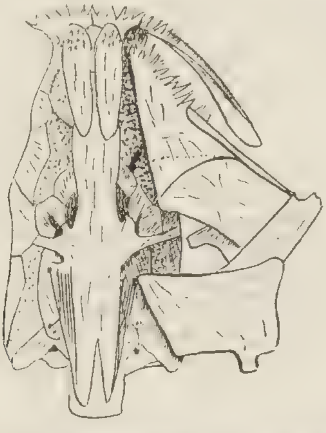


Fig. 61.—*Amia* (modified from Sagemehl.)

The third pair is developed on the upper surface of the cartilage, extending back behind the olfactory pit but having a deficiency over the pit. This pair also project forward, extending beyond the prevomers and also being broader than them. Like those bones they bear teeth. These are the premaxillae.

Both these pairs of bones might appear to be claimants for recognition as the homologue of the premaxillae of the higher vertebrata.

To my mind the evidence against the claim for the first pair is strong in the presence of the second.

Those which we have identified as the prevomers are developed below the cartilaginous solum nasi and they suture with the anterior end of the synpterygoid (parasphenoid), just as do the prevomers in the Tetrapods.

The other pair lie in essentially the position of the premaxillary bones of the Tetrapods, that is, above and in front of the ethmoid cartilage, the portion above being the ascending process. The relation of the ascending process to the nasal bone and the nasal organ is fairly well maintained. Among higher vertebrata the premaxilla may develop either a processus praenasalis or a process extranasalis, the one being medial, the other lateral to the external nares, and both being ascending processes. These processes, however, are never covered by the nasal bones; they are in the same plane as them and make sutural contact with their edges, and are placed anterior to or above the nasal organ. The two processes are present in *Amia*, but have not contributed to the side wall of the nasal organ.

I would particularly draw attention to the fact that in this, as in all other similar comparisons throughout the work, I have invoked the characteristics of whole classes in evidence, and in no case do I base any conclusion on the evidence of the anatomy of a single animal or fish.

The maxillary labials are not supported by a process of the premaxilla as in the Teleostei, but are "pegged in" as it were between the premaxillary and the prevomer. The pit into which its little peg fits is placed immediately behind the tooth-bearing area of the premaxilla and above the antero-lateral corner of the prevomer.

Lepidosteus.

The chondrocranium of this fish is, in the adult, very difficult to harmonize with that of other bony fishes. A reference to its form in early developmental stages, however, discloses close similarity to the chondrocrania of more normal adult types at similar developmental stages. From such comparison one learns that the striking peculiarities of the adult form must all be regarded as late ontogenetic and not phylogenetic features. In other words, this is an individual specialization, comparable to many that might be cited amongst the modern Teleosts.

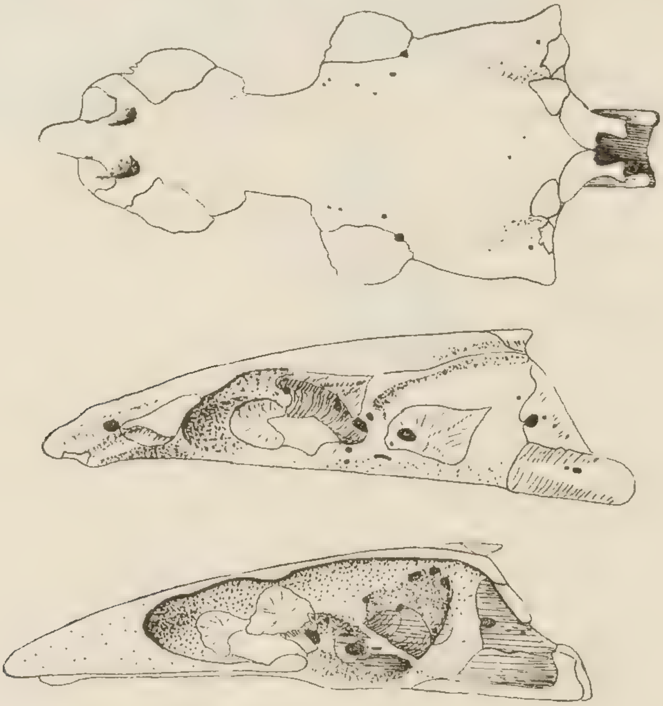


Fig. 62.—*Amia* (after Allis, 1897).

The peculiarities of the bony skull are more apparent than real. The so-called basipterygoid process is not, in the reptilian sense, a basipterygoid process at all. It is a process of the parasphenoid and prootic bones and is closely, if not absolutely, paralleled in certain of the more primitive of the Teleostei, e.g. *Heterotis, Osteoglossum* and *Arapaina* (Ridewood, 1904).

The maxillo-palatine arch is fundamentally similar to that of *Amia*, but with the individual bones altered in length by the elongation of the skull in front of the cavum cranii. The relation of the bones in the suspensorium, one to another, is quite typical. Tate Regan (1923) follows W. K. Parker (1882) in identifying the quite normal preoperculum as the interoperculum. This error was corrected by Goodrich (1909).

It is possibly only a coincidence that the three fishes quoted above as having a pseudobasipterygoid process also resemble *Lepidosteus* in the absence of an ectopalatine.

The premaxilla is apparently devoid of ascending processes, but this also is only a matter of appearance. The reduced ascending processes lie behind the nasal capsules. It differs from the ascending process of the premaxilla of *Amia* in that the median process stops short of the anterior aperture of the olfactory canal, but the lateral arm ascends to meet the nasal. The maxillary labial differs from all the other bones of this region in that, in place of being elongated to produce a single more or less splint-like bone, it has been fragmented in the process of extension. It is also different from the bone in *Amia* and the Teleosts generally, in that it is closely applied to the lateral edge of the maxilla.

There is no question that the composite bone is homologous with the single maxillary labial in the fishes generally, so that the condition is particularly interesting as providing one of the stages connecting the conditions presented in many of the Crossopterygians with those so familiar in the modern Teleosts.

The roof pattern is essentially the same as that of *Amia*. Gregory has recently identified the nasals as the ascending processes of the premaxilla. This identification leads him into the further error of identifying a little pair of dermal scales, which lie in front of the nasal capsules and between the two apertures of each, as the nasals. A small pair lying behind and lateral to these he designates adnasals, and suggests that they may be antorbitals. In this situation they differ markedly from the nasal and adnasal of *Amia*, which are said to correspond with the antorbital of palaeoniscids, which last also lies behind the nasal capsule. Inasmuch as that the nasal bone throughout the whole of the rest of the vertebrata lies above and behind the premaxilla, between it and the frontal behind it, the identification of the little scute at the anterior end of the snout of *Lepidosteus* as the nasal is surely at fault.

Gregory suggests that the tiny little dermal scale which lies between the anterior pair of prenasal scales is the mesethmoid of the Teleosts. Since it lies in front of the premaxilla and the ethmoid lies behind those bones, this suggestion is quite unacceptable.

The frontal does not, as in *Amia*, overhang the boundary of the orbit. There intervenes a series of periocular scutes which are continued right round the orbit. Behind these, and completely covering the pterygoideus and quadratomandibularis muscles and filling all the area between the orbital scutes in front, the preoperculum behind, the frontal and pterotic above and the lower arm of the preoperculum below, there is an area of irregular, small dermal scutes.

The periocular scutes are regarded by Gregory as evidence that *Lepidosteus* stands close to the Semionotids, and he says of *Amia*, that it probably stands much nearer to the base of the Teleosts than it does to *Lepidosteus*. The general implication of his remarks on *Amia* is to the effect that it stands nearer to the Teleosts than, in the past, has been admitted. Herein I am in agreement with him, but I cannot agree that the above features indicate that *Lepidosteus* is not closely related to it and that they are not rightly placed together.

Amia certainly lacks the dorsal periocular scutes, but it has the same number of post-orbitals, three, certainly much enlarged, the same number of infra-orbitals, two, and only one additional infra-preorbital. There is here no character on which to separate the two forms. The third post-orbital is attached to the dorsal edge of the maxillary labial and is termed "jugal" by Allis.

Gregory also quotes the forward inclination of the suspensorium as a character of importance indicating semionotid relationship in *Lepidosteus*. This forward inclination is far in excess of anything found in the group he refers to and is, perhaps, not of importance, the intermediate stages in forward inclination being readily obtainable amongst modern Teleosts.

The pseudobasipterygoid articulation of the metapterygoid is, on the other hand, a very striking feature. If it be also a phylogenetically important feature, then it will be necessary to transport *Lepidosteus* on this account alone, and it will be necessary to consider the claims of several of the forms allocated to the Osteoglossoidea and Mormyroidea to close relationship with *Lepidosteus*. They have not only this feature in common, but also they lack the ectopalatine as an independent ossification, and have the median edge of the maxillo-palatine arch firmly sutured to the parasphenoid.

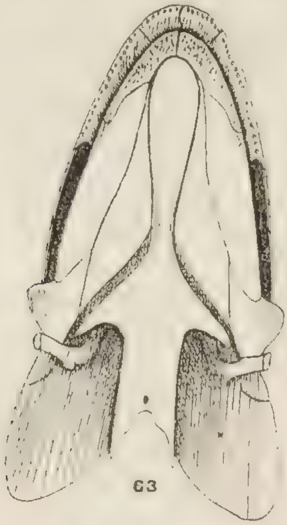
It may also be noted that *Lepidosteus* possesses a very complete primordial chondrocranium, the walls between the cavum cranii and the nasal capsules being especially well developed, almost completely enclosing the sphenoidal cavity. In this respect, again, there is a resemblance to *Gymnarchus*, the only member of the above two groups whose development has been worked out, so far as I can ascertain.

The adult chondrocranium of *Amia* so closely resembles that of *Salmo* that it is probable that its primordial chondrocranium was similarly fenestrated.

Polypterus.

(Figs. 63, 64, 65.)

The chondrocranium of the adult *Polypterus* displays a closer approach to the condition of the primordial chondrocranium of the modern Teleosts than does that of *Lepidosteus*. That this is not a late modification is clearly indicated in the larval stages. In these early stages the nasal capsule is connected to the cavum cranii by simple cartilaginous rods, trabeculae cranii and supraorbital bars (Budgett, 1907, p. 160). In the adult no trace remains of the trabeculae, and only the anterior portion of the supraorbital bars is found. In the otic and ethmonasal regions complete cartilaginous girdles are present. The former includes the otic capsule, the major portion of which persists in cartilage, the latter lodges the olfactory canals.



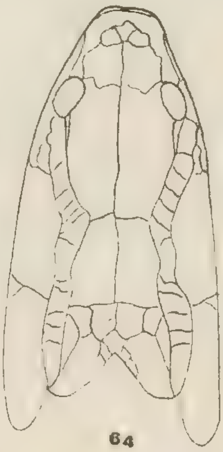


Fig. 63.—*Polypterus.*
Fig. 64.—*Polypterus* (after Gregory, 1933).

This persistence of the wide fenestration of the sphenethmoid region, so characteristic of the primordial chondrocranium, not only of the bony fishes but also of the Tetrapoda generally, might be interpreted as indicating a closer relationship to those forms than to *Lepidosteus* and other forms in which the fenestration is not so marked.

Such a view, however, would overlook the fact that this wide fenestration of the primordial chondrocranium is an early and fundamental condition of every chondrocranium.*

---

* The work of Platt, Stone, Landacre, and de Beer, demonstrating that the trabecular derivatives of the cranium are of ectodermal origin, whilst the parachordal are of mesodermal origin, completely explains the why, and largely the how, of this fenestration.

It follows that the complete chondrocranium of the Elasmobranchs, or wherever else found, is to be regarded, not as the persistence of a primitive early embryonic condition, but as the persistence of a late embryonic and adult condition.

In short, the complete is a specialized development from the fenestrated chondrocranium, is characteristic of the Elasmobranchs, and is probably an inherited character from some ancestor common to all those fishes which possess the feature.

It is realized fully that this is an almost fundamental change in our view, which has regarded the complete as the primitive chondrocranium, but it seems to follow necessarily from the facts recorded in the works quoted

It should, perhaps, be pointed out that we may not conclude from the failure to develop a complete chondrocranium in any of its stages of development, that the fish or animal being studied did not come of ancestral stock common to itself and the Elasmobranchii. The most that one is justified in concluding is that, if from elasmobranchian stock, the characteristic chondrocranial stage of that ancestral stock has been dropped from the ontogeny of the example.

The different origin of the two regions of the chondrocranium predetermines fenestration in the sphenethmoid region, so that no matter how accelerated the cranio-visceral development may be, this fundamental stage must appear if any primordial chondrocranial elements at all are developed. On the other hand, since the relatively complete chondrocranium is not primitive and fundamental, but a characteristic of the elasmobranchian stock, it gains in value as a phylogenetic feature.

Professor Gregory, whose view is largely limited by the twin hedges of the bone-paved lane the palaeontologist is constrained to travel, says (1933, p. 123), " I fail to see in the embryo Sturgeon any specially elasmobranchian characters not shown in other fish embryos . . . ". Surely the early development of a very complete chondrocranium cannot be interpreted in any other way than as indicating a close alliance with the Elasmobranchii.

The osseus palate and suspensorium are essentially similar to that of *Amia*. The premaxilla is a longer and narrow bone than in that fish and only meets its fellow along a short edge anteriorly. The wide expansion of the synpterygoid at its anterior end occupies the situation of the palatine lamina of these bones in *Amia*. The premaxillary bone is very similar to that of *Lepidosteus*. The median arm of the ascending process, present in *Amia*, is missing in this, as in *Lepidosteus*. The lateral arm is larger than in either of the other fish, and is sutured to the lachrymal (the only infra-preorbital scute present) along its inferior edge, and to the lateral edge of the nasal along its superior margin. The maxillary labial extends back beneath the orbit as in *Amia* and the Teleosts generally. Here, however, it has insinuated itself between the post-orbital scutes, so that the third lies below it, and the two upper scutes above it are much reduced. Not only is this so, but it sutures, between the scutes, with the anterior edge of the " cheek plate ", a bone which has taken the place of the shield of small irregular scutes which cover the muscles of mastication behind the post-orbitals in *Lepidosteus*.

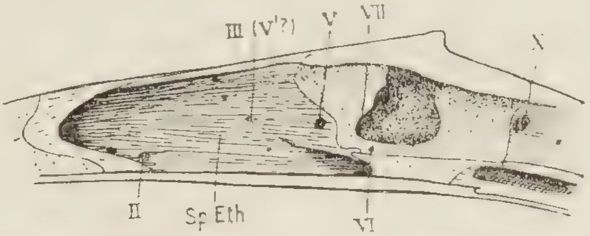


Fig. 65.—*Polypterus* (from Kesteven, 1926*b*, from Allis).

The resemblance which this labial bone in *Amia* and *Polypterus* bears to the maxillary arcade of the Tetrapods is truly extraordinary, so that the long-standing error in their identification was only natural in the absence of embryological evidence.

It must, however, be remembered that (like the labial bones of *Lepidosteus*, *Amia* and the Teleosts generally, with which they are undoubtedly homologous) they are developed quite independently of the palato-quadrate or the horizontal lamina of the ethmoid region of the chondrocranium.

The wide subotic processes of the synpterygoid present a superficial resemblance to the basipterygoid processes of the Tetrapoda and a real resemblance to the condition in *Lepidosteus*. Though the synpterygoid here makes contact with the metapterygoid and the palatine, there is neither sutural union, as in the Mormyroidea and their congeners and *Ophiocephalus*, nor an articulation as in *Lepidosteus*.

If, for the moment, we omit from the comparison the series of spiracular ossicles, the roof pattern of *Polypterus* differs from that of *Amia* in the following minor details only. The adnasals are situated in front of the nasals in place of beside them, and each tabular has been divided nearly in halves.

The spiracular ossicles, which are without close parallel in any of the known recent or fossil fishes, and the division of the tabular give to this roof a primitive appearance decidedly suggestive of close alliance with the crossopterygian fishes rather than with the actinopterygian. This resemblance is heightened by the presence of the large cheek plate and the two gular plates, and is still further increased by the sutural union of the maxillary labial with the infra-post-orbital dermal bone, the cheek plate.

Unfortunately our knowledge of the fossil Crossopterygii is largely confined to the external features of the skulls, and these are so exceedingly variable that it would appear that every new form described provides another pattern in the number and arrangement of the dermal scutes. Amongst this maze of dermal scutes and varying relation with the labial bones it has proven difficult to seize on anything of demonstrably valuable phylogenetic significance.

In only a very few instances have we any thoroughly reliable information as to the structure of the palate and the bones of the cavum cranii, and the relation of the latter to the former.

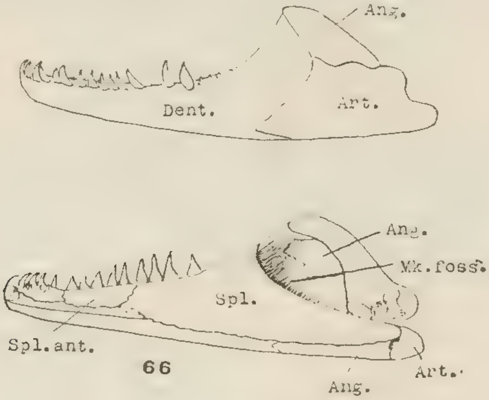
If the most recent interpretations of these few examples are correct and truly representative of the Crossopterygian fishes as a whole, then very assuredly *Polypterus* is infinitely more closely related to the Actinopterygii than to them. Compare in this respect especially the recent interpretation of the palate of *Eusthenopteron* by Watson and by Bryant.

Quite apart, however, from the resemblance, fancied or otherwise, to the crossopterygian fossils, the essential similarity of the cranial structures of *Polypterus* to those of *Amia* and *Lepidosteus* must surely be accepted as indicating a closer relationship between the three forms than has been admitted in the past.

Appendix A.

THE ELEMENTS OF THE LOWER JAW IN THE BONY FISHES.*

The lower jaw of *Scomber*, as figured by Allis (Fig. 66), may be accepted as representing quite typically the normal for the Teleostei. There is a good deal of variation in the relative size of the two larger components, though in the great majority of instances the dentary is the



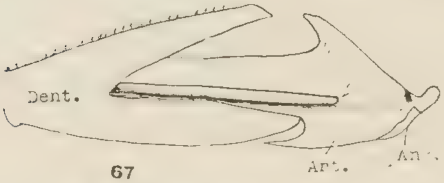


Fig. 66.—*Scomber* (after Allis).
Fig. 67.—*Amia* (after Allis, 1897).

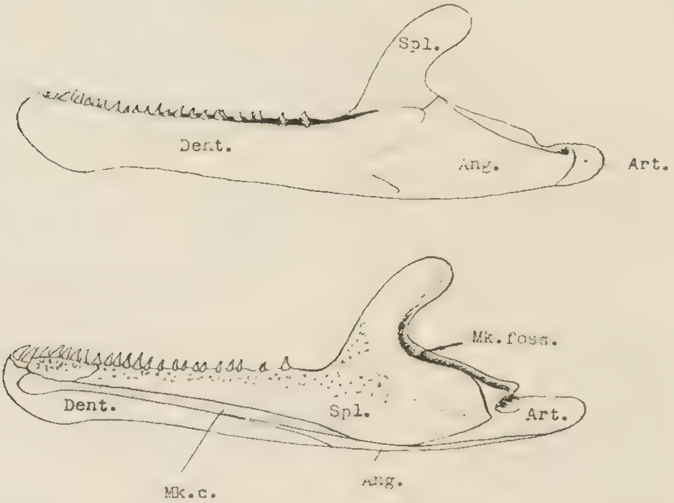


Fig. 68.—*Polypterus* (after Allis, 1922).

---

* I have examined the branchial skeleton of a number of fishes, both elasmobranchian and bony, and have been unable to seize upon any features of general morphological interest; they are therefore not reviewed in this work. I would not be understood to assert that these structures are not capable of yielding evidence of general interest, but simply that I have failed to find such evidence. Whether that failure is due to want of interest or fuller knowledge or is really not available I leave the future to decide.

larger. It is common for the dentary to be extended back along the inner side of the articular so as to convert the sulcus along which Meckel's cartilage lies into a canal. This, in the section dealing with the muscles, has been termed Meckel's canal and the posterior opening has been termed Meckel's fossa. The fossa is more or less completely closed, in the flesh, by the tendinous insertions of the pterygoideus and quadrato-mandibularis muscles. When, as in *Scomber*, the canal is widely open for the greater part of its length, it is usually filled by the quadrato-mandibularis inferior. The coronoid, or ascending process of the lower jaw, may be formed by the articular or by the dentary, or by both.

It is of particular interest that all the more primitive fishes have a more complex ossification of the lower jaw than have the Teleostei.

Amia and *Polypterus* (Figs. 67, 68).—My drawings are reproduced from the work of Allis. It is believed that these are sufficiently explanatory to need no further comment. The lower jaw of *Lepidosteus* is essentially similar to that of *Amia*. The bone which Parker (1882, p. 479) terms the coronary is that which Allis identifies as the largest piece of the splenial.

The complex structure of the lower jaw of *Eusthenopteron* was described by Bryant (1919). I reproduce his illustrations. Here again further comment appears uncalled for (Fig. 69A, B).

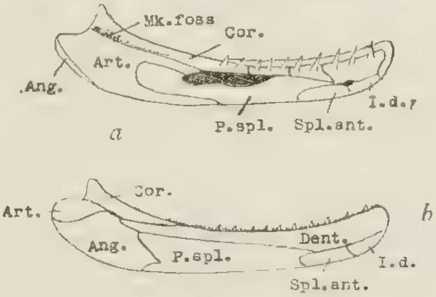


Fig. 69.—*Eusthenopteron* (after Bryant, 1919).

Appendix B.

THE TEETH OF THE FISHES.

It is not proposed in this section to describe any of the very many forms of teeth and their various relations to the bones of the palate, upper and lower jaws, and labial bones. Their variety is so extensive that it were a lengthy work to review even the commonest of them.

The palaeontologist, perhaps to some extent obsessed by the importance of tooth form in the higher vertebrates, has in several instances sought to support arguments as to the phylotic relations of the lower vertebrata, one to another and to the higher vertebrata by citation of similarities in tooth form and relation to the bone.

It were a foolishness to deny the importance of the form of the teeth in the determination of phylogenetic questions as between the members of the higher Tetrapoda, but it is quite certain that these characters become successively less reliable as we descend the scale, and he were a brave man who would attempt to determine the relation of the Crossopterygii to the Tetrapoda or the Dipnoi to the Amphibia on the form of the teeth, their mode of implantation on the bone or cartilage, or their presence or absence on specified bones.

On such evidence as this we should divorce some of the larval siluroids from the adult, the one has sharp spiny teeth lightly set in cup-like depressions, the other short blunt grinding teeth deeply set in sockets. Some of the recent Acanthopterygii have sharp tearing teeth along the outer edge of the labial and dentary bones and grinding plates on the maxilla. The majority of these fish have the teeth set in sockets of varying depth. In the great majority the socket is cup-like, and the teeth are shed and replaced, but in some it is of such depth that there is little room for doubt that the tooth is never shed, but grows continuously through the life of the fish. In the Plectognathi the teeth are developed quite superficially on the outer surface of the labial bones, a method of development entirely different from that of the Teleostei generally.

As an instance of wide variation in dental characters in closely allied fishes one may quote the members of the Blennioidei (Gregory, 1933, pp. 374-37).

Finally, the extreme variability of dental characters among closely allied fish may be illustrated by citation of the many forms of teeth present in the different batoid Selachians, and of the variety of teeth which gave their name to the " heterodont " Selachians.

THE HOMOLOGIES OF CERTAIN OF THE BONES IN THE SKULL OF THE BONY FISHES.

In the foregoing pages a nomenclature for the bones in the palate and for some of those in the skull has been employed which is quite at variance with the commonly accepted nomenclature and its implied interpretation of the homologies of the bones concerned. This nomenclature is the outcome of studies whose results I have published in various papers during the last twenty odd years. There follows here a review of the facts of development, and adult anatomy, both of the recent and fossil forms, which, in my opinion, support the conclusions I have arrived at.

The Evolution of the Superior Maxillary Bones.

The key to the understanding of the evolution of the two superior maxillary bones is to be found amongst the Elasmobranchii. The Plagiostomes probably present the primitive condition. In these fish the mouth is formed directly around the epi- and cerato-mandibular cartilages, the quadrato-mandibular and Meckel's cartilage. The vestigial, extra-, pharyngo- and hypo-mandibular cartilages simply lie amongst the tissues of the cheek and take no part in the formation of the mouth (Figs. 30, 34).

The Chondrostei present a further stage, the end stage along this line of evolution. In them, it will be remembered, the labial cartilages have been lost entirely.

It is a peculiar fact, however, that, although not ancestral to either the Crossopterygians or the Tetrapods, the Acipenserids have developed a true maxilla upon the quadrato-mandibular arch. This bone has always been designated " maxilla ", but there can be no doubt that it is not homologous with the maxilla of the modern bony fishes.

The inception of the maxilla and premaxilla of these latter is to be seen in the Holocephali. Here we see the labial cartilages impressed into the formation of an added fore part of the mouth, in front of the jaws. This added portion is, of course, the mobile upper lip, prehensile in these cartilaginous fishes as in the Teleostei. It is of particular interest to observe that the movements of this lip are brought about by specially modified portions of the superficial, temporo-masseteric, division of the masticatory muscles (Fig. 20).

Turning next to the Teleostei, it is found that the labial cartilages have but a transient embryonic independence, and early become incorporated into the premaxillae and maxillae which are otherwise largely developed as membrane bones (Norman, 1926). Again we observe that these labial bones are moved by specially modified portions of the temporo-masseteric muscle (Figs. 27, 28, 29).

Apparently these labial bones were developed in the ancestors of the Amphibians, for we, undoubtedly, are able to observe their elimination from the armamentarium of the Anura during the later stages of the metamorphosis of the tadpole. The labial cartilages are present, armed with teeth, working against the Meckelian lower jaw and activated by the same portion of the temporo-masseteric group of muscles in the fully developed tadpoles of all Anura (Figs. 75, 76). During the late stages of the metamorphosis the cartilages are absorbed, and their muscle gains a new insertion into the lower jaw.

This, apparently, is the history of the evolution and abolition of the labial bones which have, in the past, been regarded as the maxillae and premaxillae of the Teleostei.

We turn next to the evolution of the true superior maxillary bones.

The discovery of *Latimeria*, a more primitive crossopterygian than *Polypterus*, provides the earliest stage in the evolution of these bones amongst the living vertebrates. Here we find that there are two aggregations of tooth-bearing ossicles related to the anterior end of the palato-quadrate arch anteriorly.

In *Polypterus* (Fig. 63) and early, Triassic, crossopterygians such as *Eusthenopteron*, and *Osteolepis* these aggregations have taken on the form of the tetrapod maxilla and premaxilla.

Amia, Polypterus, and some of the Actinopterygians present a combination of the two forms of jaw-bones, and it is just the existence of these intermediate forms which has been responsible for the past misunderstanding of the bones. These fish have retained the labial maxilla and have anchored its anterior end between the true premaxilla in front and dermal bones behind it (Fig. 61). The extraordinary resemblance of the resulting combination to both the labial type of jaw on the one hand and the true jaw on the other has been the cause of the misunderstanding.

Up to this point the embryological evidence has not been stressed because it was felt that the question was one which was likely to interest the palaeontologists, and that, therefore, the case for this interpretation of the bones should be presented, as far as possible, on the evidence of adult form, for that, unavoidably and very naturally, is the form of evidence which our palaeontological colleagues best understand. There is, however, no little embryological evidence in favour of the above interpretation.

Basically, there can be no doubt that the manner of development of bones is not a haphazard process, but is one which has been inherited in perfectly orderly fashion along with other features and functions. Therefore, if we can show that the labial bones develop in a manner and in a location quite different from that of the jaw bones of the Tetrapods, this must be accepted as evidence that the bones are not homologous.

There is little reason to doubt that the pair of upper labial cartilages so commonly present in the Teleostei are completely homologous with those of the Selachii.

Now it has been demonstrated that the premaxilla of the Teleostei develops in relation to the anterior of these cartilages, but that the bone develops largely as a membrane bone (Swinnerton, 1902; Gaupp, 1906; Norman, 1926). The cartilage itself is designated "premaxillary" by de Beer (1937). The posterior cartilage was designated the "maxillary" cartilage by Sagemehl when he found that the maxilla was developed in relation to it (Sagemehl, 1885, 1891).

In the Ganoid fishes these cartilages have not been detected, and it might, therefore, appear that here is evidence that the bone which has been identified as the maxilla cannot be the homologue of the maxilla of the Teleostei. This does not follow because, in quite a number of the modern Teleosts, neither of the labial cartilages appears to have been developed, yet there can be no question as to the homology of the labial bones in all of them.

Perhaps a moment's consideration of the phenomena of the early differentiation of the osteogenetic tissue will help to clear the position.

Dantschakoff (1909) demonstrated that osteogenetic tissues were precisely similar, whether differentiated in relation to cartilage or not. Stump (1925) stated that the evidence of histology very definitely indicated that the cartilage related to developing bone took no part or share in the actual bone formation, that it was simply replaced by the bone. Its only function was to provide a model, as it were, on which the future bone was to be formed. Kesteven, from an extensive survey of the process of ossification of the Saurian basis cranii (1940) and more particularly from a survey of the ossification of the Avian chondrocranium (1941) arrived at the same conclusion.

It appears that when once the site of the differentiation of osteogenetic tissue has been determined, this ontogenetic habit at once becomes more or less fixed.

We may, however, go further. In view of the fact that the cartilage takes no part in the formation of the bone which develops in relation to it, it is quite reasonable to believe that, once the site of the differentiation of the osteogenetic tissue has been determined, the loss of the cartilage to which it was originally related need not have caused any appreciable change in the development and form of the bone itself. Amongst the fishes themselves the fact that, even in the presence of the cartilage, the bones are developed largely as membrane bones, is evidence of a certain established degree of independence of the cartilage in the osteogenesis; so that the development of the bones in the absence of the cartilage is quite understandable.

What appears to be another illustration of the same thing is the regular development of the supraoccipital bone, whether a precursory tectum synoticum was developed or not.

It follows from what has gone before that there is complete justification for accepting as homologous the maxillae of Ganoids such as *Polypterus* and *Amia*, and those of the generality of the Teleostei.

It would seem, also, to follow that the premaxillae in these Ganoids were homologous with those of the Teleostei, differing only in that they are developed in the absence of the cartilage. Undeniably this line of reasoning is open to us, but it is believed that other evidence is stronger and leads to its rejection. But, before proceeding to that other evidence, it is as well to follow the above line of reasoning to its logical conclusion.

If it be assumed that the maxillae and premaxillae of such forms as *Amia* and *Polypterus* are homologous with the labial bones of the Teleostei, it will be assumed that the process of their evolution has been as follows. The labial cartilages have been lost and the labial bones formed entirely in membrane. The premaxillae have then come to acquire a new relation to the anterior end of the ethmoidal cartilage and the maxillae to the lateral margin thereof. Finally, in this new situation, they have attained to the position of the tetrapod bones of the same name.

Though, apparently, this line of reasoning has not, heretofore, been clearly stated, it is, in fact, the line of reasoning which underlies the commonly accepted homologization of the bones in question. The only alternative is an assumption that the labial bones of the Teleostei have been evolved in the directly contrary way, by some process of liberation from the true arch of the jaw, and for this assumption there is not one scintilla of evidence.

The above statement of the argument in support of the accepted interpretation of the bones is entirely reasonable and tempting, but it is open to weighty objections.

The most important of these is the history of the ontogeny of the maxilla and premaxilla in the Anura. There is no room for doubt that these bones in the Anura are completely homologous with those of the rest of the Tetrapoda.

The condition in the early tadpole is myologically almost as primitive as that of the Holocephali. There are present, in front of the ethmoid cartilage, two superior labial cartilages hinged to one another and to the ethmoid cartilage essentially similarly to the labial bones in the Teleostei. These two cartilages constitute, and function as, a prehensile, biting upper jaw. They are activated by a completely separate portion of the temporo-masseteric masticatory musculature, just as are the labial cartilages in the living Holocephali but, in these last, it is a part of the pterygoid muscle which acts upon the labial cartilages. During metamorphosis, for a fleeting period, the myological conditions reproduce with *complete faithfulness* those of the Teleostei. The retractor labii superioris gains a new insertion into the lower jaw. This is the condition found in every one of the fishes which possesses the mobile labial bones. The superficial portion of the temporo-masseteric muscle is inserted into the lower jaw at the coronary process and has also a strong tendinous insertion onto the maxilla, acting as a retractor labii superioris. Following this stage, the superior labial cartilages are completely absorbed, the muscle retains only its insertion into the lower jaw, and the maxilla and premaxilla are developed, as in all other Tetrapoda, in close relation to the ethmoidal cartilage and/or its processes, and the anterior attachment of the palato-quadrate.

There appears to be only one interpretation of this history. It is that the superior labial cartilages and their muscles have been inherited directly from some piscine ancestor. The cartilages are, therefore, almost without doubt, completely homologous with those of the fishes. If this be the fact, then it is out of accord, in important respects, with the history of the evolution of the tetrapod maxilla and premaxilla, as outlined above, in conformity with the generally accepted interpretation of the bones.

In the Anura, not only is there no trace whatsoever of bone development in relation to the cartilages (which, had it been there, might later become related to the ethmoid cartilage), but actually the osteogenetic stroma of the future maxillae and premaxillae is clearly recognizable in close association with the ethmoidal cartilage, whilst yet the labial cartilages are functioning as the jaws.

Since the cartilages are homologous with those of the fishes, they must also be homologous with the bones which are developed in relation to them.

Here, it seems, is the complete evidence that in the Anura, at least, the maxillae and premaxillae are not homologous with the bones so named in the Teleostei.

It is doubtful if anyone will deny the homology of the Anuran bones with those of the rest of the Tetrapoda. It follows, unavoidably, that the maxillae and premaxillae of the Tetrapods are not homologous with the bones so named in the Teleostei.

It is probable that the premaxillae of Ganoids such as *Amia* and *Polypterus* have been developed in the same manner as in the Tetrapods, from a beginning such as is seen in *Latimeria*, and the form of the lip folds in *Latimeria* suggests that some trace, perhaps in cartilage only, will be found of the labial skeleton, when more and better preserved material is examined.

Turning again to the Teleostei, there is related to the anterior end of the ethmoid cartilage a bone which has been termed the vomer. Although, apparently, this designation has never been challenged, it has for many years now been used merely as a convenience. In our almost universal acceptance of Sutton's interpretation of the origin of the vomer, we have all tacitly admitted that this piscine vomer could not have been homologous with the bone so named in all other vertebrates. Westoll and Parrington (1940) have recently advanced very strong evidence that we have all been in error in our acceptance of Sutton's equation, and Kesteven's (1941) demonstration that the so-called rostrum basisphenoidei of the Saurians is a presphenoidal ossification and not parasphenoidal, is strong confirmation of their conclusions.

It will, probably, be agreed that if there were no labial bones in front of this " vomer " in the fishes, it would be identified unhesitatingly as the premaxilla, and there would not be one single feature in its development and adult location out of congruence with such an identification.

This " vomer " has, in recent years, been designated " prevomer " by some writers, but this is an unsatisfactory identification. The prevomers of the Tetrapoda are situated further back, and never extend onto the dorsum of the ethmoid cartilage as this bone so commonly does.

Having taken cognizance of this bone, and recognizing that it is always present in the osseous cranium of the fishes, we have now to add another clause to the line of reasoning which equates the labial bones of the fishes with the maxillary bones of the Tetrapoda. This new clause runs as follows : As the premaxillary labial bone came to gain its new relation to the anterior end of the ethmoid cartilage, it displaced backwards the bone which previously occupied its new position. This clause is necessary in any case, but more so if the " vomer " of the fishes is to be equated with prevomer of the Tetrapods.

This is an unfortunate addition to the argument, for it overloads it. It is hard to understand why, if the cranium was already strongly supported by a well-established bone, another should have taken its place and caused it to migrate backwards.

The weight of the evidence points to the probability that the " vomer " of the Teleostei is in reality the tetrapod premaxilla.

THE MAXILLA.

It has just been demonstrated that there is every probability that the labial bone which has been regarded as the maxilla in the bony fishes is in reality the homologue of one of the superior labial cartilages of the Amphibia. It remains to inquire for, and, if possible to identify, the maxilla of the Tetrapods in the fishes.

The maxilla in the Amphibia and Reptilia is developed in relation to the lateral and ventral walls of the nasal capsule and also in relation to a backwardly projecting " posterior maxillary process " (Gaupp, Fig. 383) of the capsule in the reptiles.

Swinnerton, describing the development of the palatine bone in *Gasterosteus* (1902, p. 545), says : " The (cartilaginous palatine) process is, relatively, much slenderer than at any previous stage, and its extremity, owing to continued growth of the maxillary process, is expanded. Behind this the cartilage is not merely in contact, but in actual continuity with that of the pre-ethmoid cornu. The palatine bone surrounds this point, and extends back almost to the level of the parethmoid." It is, then, around the anterior end of the palato-quadrate arch that the palatine, so-called, in the fishes is developed.

The union of the fore end of the palato-quadrate with the ethmoid cornu appears to be a very primitive feature. I have previously noted that " It is of constant occurrence throughout the Anura, very generally present in larval stages of Urodela, and in those urodeles in which the continuity is broken there is, as also in the gymnophiones, evidence that such continuity has been but recently lost from the ontogeny. The anterior structural continuity of the palato-pterygoid and the ethmoid plate has been recorded in several Teleostei, as a temporary condition in embryonic life, and among the elasmobranchs it is found in the adult Holocephali, and it is not improbable that the anterior articulation of various Selachians will be found to have been preceded by cartilaginous or procartilaginous continuity, as demonstrated for *Acanthias* by Sewertzoff (1899). Among surviving ganoids, *Lepidosteus* is apparently alone in presenting the continuity here under review " (Kesteven, 1931*a*).

In the Anura the fore end of the palato-quadrate cartilage is pinched off and remains as a posterior maxillary process attached to the postero-lateral corner of the solum nasi. This is apparently quite constant among the anurous amphibians. Parker describes and depicts it clearly in Rana (1871), and I have been able to study the development of *Lymnodynastes, Hyla, Crinia* and *Myxophyes*, and find the same thing in all four. Gaupp designates the cartilaginous piece in question, processus maxillaris anterior and posterior of the planum antorbitale (Handbuch, p. 735).

There is little reason to doubt that the processus maxillaris posterior of the reptilian chondrocranium is completely homologous with that of the amphibian, and this, at times, if not always, is demonstrably derived from the fore end of the palato-quadrate cartilage.

Since it is in relation to the two processi maxillares that the maxilla is developed in the lower Tetrapods, and since these are probably homologous with the fore end of the palatoquadrate, around which the so-called palatine of the fishes is developed, it would appear only reasonable to conclude that this bone is homologous with the maxilla of the Tetrapods and should be designated in accord with its homology.

It may be remarked, before leaving this subject, that the position in which this bone is developed is emphatically not one that would justify its identification as the palatine, as in the past.

THE PALATINE.

That which is here identified as the palatine bone in the fishes is the bone that has heretofore been designated meso- or entopterygoid.

The palatine bone in the Tetrapods is a membrane bone situated rather far back in the palate. Of this bone in the reptiles, Williston (1925, p. 20) wrote: " Primitively forming the posterior boundary of the internal nares, articulating with prevomers and pterygoids on their inner sides, the maxillae on their outer, and with the descending process of the prefrontal above ".

In the Amphibia there is a relatively wide range of variation in the situation and relation of the bones which have been designated palatine. In the Anura the bone is constantly a narrow splint which develops along the infero-posterior and medial concave edge of the posterior maxillary process, and in the adult is found lying along the anterior margin of the suborbital vacuity as a bony margin to the postero-lateral edge of the palate. In this situation its development resembles closely that of the " mesopterygoid " of the fishes.

In the Urodela the palatine develops further forward, on the inferior surface of the solum nasi. In some instances, e.g. *Sieboldia maxima* and *Menopoma alleghaniensis* (Parker, 1882), it is placed medial to and in front of the internal nares, in the adult of *Triton* and *Amblystoma* it is fused with the prevomers, but in larval stages it is found as a separate ossification, behind the prevomer and medial to the internal nares, developing in the situation of the inner end of the bone in the Anura.

In the Coecillians the palatine is placed lateral to and behind the internal nares, has a long suture with the maxilla, and may suture with the prevomer both in front of and behind the choanae (Wiedersheim, 1879). In these Amphibia, as in the reptiles, the bone apparently develops independently of a cartilaginous basis.

In the embolomerous Amphibia the palatine lies behind the prevomer between the pterygoid and the maxilla. Apparently in some forms it supplied the posterior boundary to the choanae, in others that boundary was supplied by the prevomer, *Pteroplax* (Watson, 1912).

In the reptiles the palatine is always a membrane bone, developed without any relation whatsoever to any chondrocranial structures. As stated by Williston, it commonly, and probably primitively, bounds the choanae posteriorly, but in some forms, e.g. crocodiles, it lies below and in front of them.

Although thus completely divorced from any cartilaginous basis, there is little reason for believing that the palatines of the reptiles are not homologous with those of the amphibians.

It must be admitted that, except for the position of the developing bone in the Anura, there is little in this review of the palatine bone in the reptiles and amphibians to support the identification which heads this section. On the other hand, there is nothing in the history of the development of the bone in those two tetrapod groups, or in its relation to other bones and skull areas in the adult, to indicate that the identification is in error.

Since the developmental evidence is not convincingly strong either to prove or disprove the identification, one is constrained to examine the adult relations of the bone. Though this kind of evidence is not so convincing as positive embryonic evidence can be, it is the only method available to the palaeontologist in identifying the bones in the fossils, and it has not often misled him.

We may define the palatine bone as a component of the palate in its posterior part, developed either quite independently as a membrane bone or in relation to the fore end of the palatoquadrate cartilage and/or the posterior margin of the solum nasi, or to the ventral surface of the solum nasi at varying distances from its posterior margin. In the adult it sutures with the palatine plate of the maxilla and usually lies posterior or posterior and lateral to the prevomers when they are developed. Exceptionally the palatine bones lie ventral to the prevomers. When, as in some reptiles and higher vertebrates, the bone extends posteriorly to the nasal chamber, it may or may not suture with the prefrontal, and in the absence of the prevomers the bones meet in a common suture along the mid-line and suture with the ventral edge of the vomer.

There is no nasal capsule, in any way comparable with the complex capsule of the amphibians and reptiles, developed in the fishes, and, probably correlated with that absence of complexity, there are no prevomers developed in the fishes' skull.

We have, therefore, left us, as landmarks for the identification of the palatine, only the maxilla and general location in the palate.

These are such that the so-called mesopterygoid is the only bone in the fish palate which can be considered. When to this, admittedly unsatisfactory, evidence we add the meagre support of the situation of the developing bone in the Anura, it would appear that we must conclude, either the mesopterygoid is the homologue of the palatine of the Tetrapods or this latter bone is not present in the palate of the fishes, and the mesopterygoid is without an homologue in the palates of the higher vertebrata.

The Ectopterygoid.

This is the bone which has been designated pterygoid and ectopterygoid.

In the original presentation of my ideas on the homology of the several bones of the fishes' palate, I identified this as the quadrato-jugal of the Tetrapods (Kesteven, 1922, p. 321). Later (1926, p. 217) I wrote: "It is now realized that this identification is incorrect; its position medial to the muscles of mastication is alone sufficient proof that the bone cannot be the quadrato-jugal."

A wider experience and more intimate knowledge of the related structures and their development gained by the study of much of the material that forms the basis of this work now leaves me once more undecided on this question.

Were Allis correct in his identification of the maxilla of *Lepidosteus* as the true homologue of that of the Tetrapods (Allis, 1900, 1919), then were it easy to satisfy ourselves that the jugal and quadrato-jugal of the Tetrapods are derived from certain of the cheek plates.

Not having had the opportunity of studying any stages in the development of *Polypterus* I accepted Allis's interpretations, and, as a further result of those uncritical readings, also accepted (Kesteven, 1931) Gregory's identification of the cheek plates (Gregory, 1915, 1920), one of which he identified as the jugal.

Since, however, the maxilla of *Polypterus*, and the Chondrostei generally, is not the homologue of that of the Tetrapods the question is not so easy of solution. The anterior attachment of these scutes to the labial bone, so-called maxilla, now becomes a reason why we should hesitate to accept their identification as jugal. On the other hand, the suture with the lacrhymal, assuming that is correctly identified, in front and with the squamosal, preoperculum, behind, are relationships which support the identification.

There is another aspect of the question that should not be lost sight of. It would appear that with the labial bones functioning as the upper jaws there is correlated, in the bony fishes, a narrowing of the maxillo-palatine arch behind and between them; this narrowing is not observable in any other forms, except as individual specializations. The true premaxillae and maxillae have persisted as the lateral and anterior limiting bones of the arch. In the great majority of the higher vertebrates there has been, on the other hand, a constriction of the arch posteriorly, to accommodate the muscles of mastication, to obviate their bulging beyond the general contours of the skull, and to permit of their direct action between fixed and moving points. In the result, the posterior end of the maxilla projects more or less outside the lateral margin of the muscles.

It is not inconceivable that the so-called ectopterygoid of the fishes retained its anterior relation to the maxilla and palatine, and came to project backwards laterally to the muscles, just as the maxilla itself has done. If so, it should be identified as the quadrato-jugal.

I know of no evidence which will satisfactorily decide the question between these two claimants for recognition as the quadrato-jugal, and, inclining to accept Gregory's identification, and because of that inclination, I have retained the designation ectopterygoid, believing that the resemblance to the os transversum of the lower Tetrapoda justifies the designation in the present state of our knowledge.

THE PHYLOGENY OF THE FISHES.

The two groups of outstanding interest in a phylogenetic review of the fishes are the Holocephali and the Chondrostei. They are of interest as much, if not more, for the light they throw on the origin of the Elasmobranchs as for the light they throw on the evolution of the bony fishes.

Taking the Holocephali first, we may tabulate their elasmobranch and teleostome features.

Elasmobranchian Characters.

Complete cartilaginous cavum cranii.

Entire absence of ossification of the skull.

The possession of a sphenoidal extension of the cavum cranii.

The possession of a relatively complete cartilaginous nasal capsule.

The form and attachments of the following muscles: epiarcualia obliqui, epibranchial spinal, coraco-mandibularis, and hypobranchial spinal.

Teleostome Characters.

The widely open lateral cranial fenestra displaying much of the structure of the otic labyrinth.

The branchial arches, gathered together beneath the skull and under an "opercular" fold.

The pharyngobranchial cartilages, fused to form a dorsal pharyngeal cartilage essentially similar to the bone of that name.

There is no spiracle.

The form and attachments of the following muscles: levatores arcuum branchialium, the levator operculi, the protractor hyoidei, and the sphincter oesophagi.

It is of interest to note that there is also this duality of characteristics in features beyond the head, the one set indicating close phylogenetic relation to the rest of the Elasmobranchs, the other indicating relationship with the Teleostomi (Bridge, 1904, p. 467; Kesteven, 1933, pp. 443-474).

Turning next to the Chondrostei, we tabulate their conflicting characteristics in like manner.

Elasmobranchian Characters.

Complete cartilaginous cavum cranii.

The form of the suspensorium.

Primitive palato-quadrate upper jaw.

The possession of a typical levator hyomandibularis muscle.

The possession of a branchio-mandibularis muscle.

The form of the protractor hyomandibularis, unquestionably a modified levator maxillae superioris of typical elasmobranch pattern.

The form of the pterygoideus muscle.

The features of the origin and distribution of the cranial nerves (Norris, 1925).

Teleostome Characters.

The presence of true ossification in membrane related to certain skull areas and visceral elements.

The widely open lateral cranial fenestra.

The form of the levatores arcuum branchialium muscles.

The absence of intrabranchial muscles and the presence of a ventral transverse branchial muscle, and of three subarcualia obliqui.

The peculiar dermal scales, with their basal layer of true bone, which are present as covering bones for the head and are also present along the side and dorsum of the body of the Sturgeons, may be regarded as teleostome or elasmobranchian features, according as we stress their superficial or deep layer.

It will appear later that the Holocephali also present features which are very strongly suggestive of close phyletic relation to the Dipnoi.

When thus reviewed, at close quarters as it were, the fishes appear to divide themselves into two great divisions, the Elasmobranchii on the one hand, and the Teleostomi on the other, with two smaller intermediate groups between their extremes.

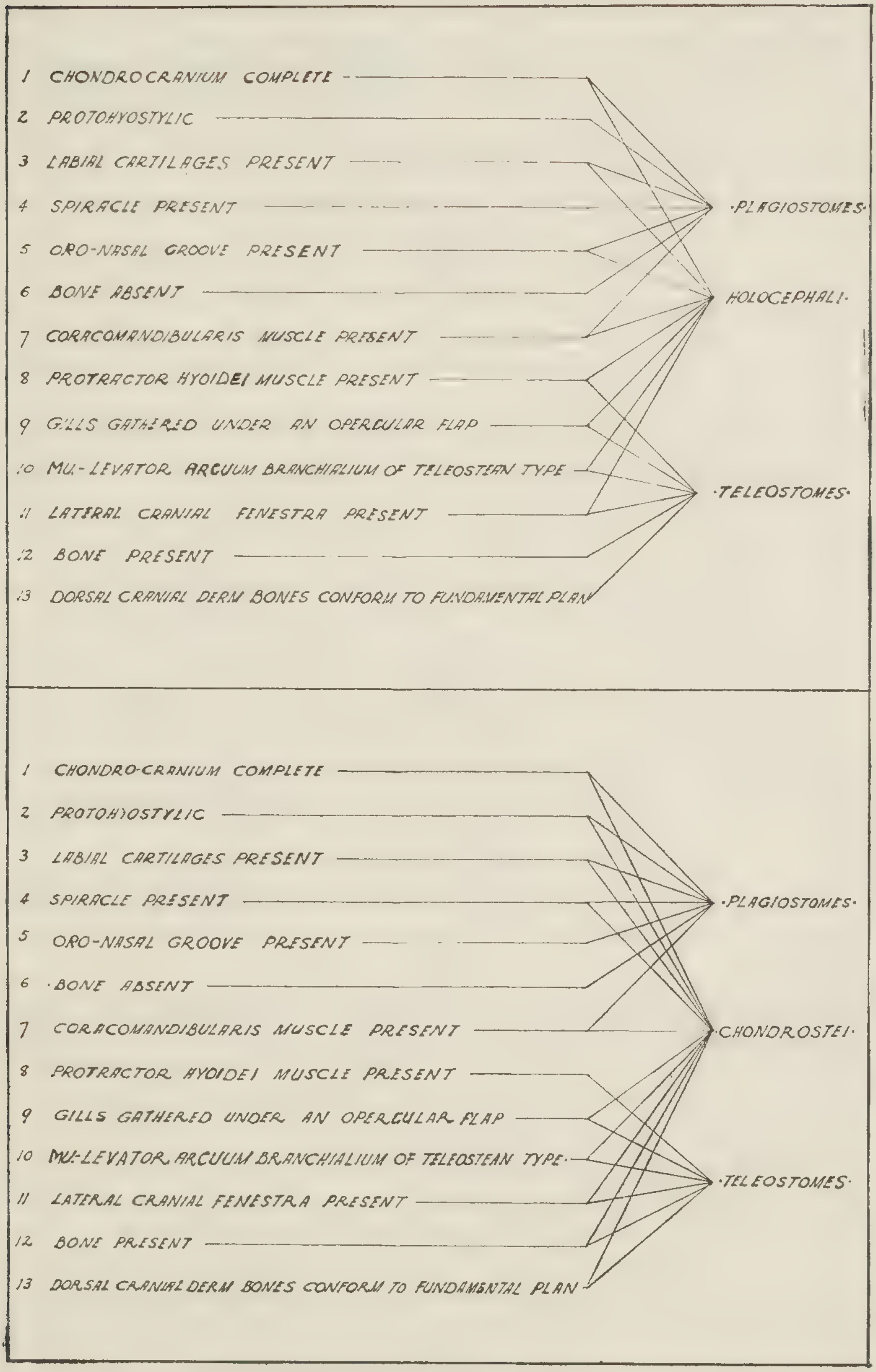

1 CHONDROCRANIUM COMPLETE
2 PROTOHYOSTYLIC
3 LABIAL CARTILAGES PRESENT
4 SPIRACLE PRESENT
5 ORO-NASAL GROOVE PRESENT
6 BONE ABSENT
7 CORACOMANDIBULARIS MUSCLE PRESENT
8 PROTRACTOR HYOIDEI MUSCLE PRESENT
9 GILLS GATHERED UNDER AN OPERCULAR FLAP
10 MU.-LEVATOR ARCUUM BRANCHIALIUM OF TELEOSTEAN TYPE
11 LATERAL CRANIAL FENESTRA PRESENT
12 BONE PRESENT
13 DORSAL CRANIAL DERM BONES CONFORM TO FUNDAMENTAL PLAN
·PLAGIOSTOMES·
HOLOCEPHALI·
·TELEOSTOMES·
1 CHONDRO-CRANIUM COMPLETE
2 PROTOHYOSTYLIC
3 LABIAL CARTILAGES PRESENT
4 SPIRACLE PRESENT
5 ORO-NASAL GROOVE PRESENT
6 ·BONE ABSENT
7 CORACOMANDIBULARIS MUSCLE PRESENT
8 PROTRACTOR HYOIDEI MUSCLE PRESENT
9 GILLS GATHERED UNDER AN OPERCULAR FLAP
10 MU.-LEVATOR ARCUUM BRANCHIALIUM OF TELEOSTEAN TYPE·
11 LATERAL CRANIAL FENESTRA PRESENT
12 BONE PRESENT
13 DORSAL CRANIAL DERM BONES CONFORM TO FUNDAMENTAL PLAN
·PLAGIOSTOMES·
·CHONDROSTEI·
·TELEOSTOMES·

Diagram I.

This view of the fishes is, it is submitted, largely caused by the marked numerical superiority of the two extreme groups. Their bulk has dwarfed, and to some extent distorted, the other two. If, for the moment, we wash from our memory all but a selection of Elasmobranchs and Teleostomes, numerically no greater than the Holocephali or Chondrostei, the four groups appear in different perspective. They now present themselves as four equally important, equally divergent, groups of fishes. It at once becomes increasingly apparent that each group is monomorphic, each is a phyletic entity.

We are now able to stand afar off, on the ancestral side of all four, and to regard them as independent, separated, groups of descendants from some one common ancestor, realizing that in the course of their evolution, whilst all have carried forward certain established features in common, each has acquired new characters peculiar to its own group.

Coming closer to the individual groups again we recognize indubitable elasmobranchian characters in three of them, and on that account I have, in the past, been inclined to group these together as being more closely related one to another than to the fourth.

Systematists, generally, have agreed that the Holocephali should be regarded as a section of the Elasmobranchs, and the Chondrostei as a section of the Teleostomi. Phylogenetically, both attitudes are probably incorrect.

I would especially point out that up to a certain point it is possible to regard the Holocephali as boneless teleostomes, and in similar fashion to regard the Chondrostei as bony elasmobranchs. Again, if we change the perspective once more and, going round them, as it were, view these fish groups from the "tetrapod" standpoint, that is, look back on them as possible ancestors, we shall at once find the Holocephali to be a long way the closest to us, at least in many of their cranial and cephalic musculatural features.

In these particular features they appear as though they had been hastening along the "amphibian" road whilst still they were elasmobranchs.

To my mind the overlapping of the distinguishing characteristics of the Elasmobranchs and of the Teleostomi in the Holocephali and Chondrostei points to the following conclusions.

The primitive gnathostome was a very generalized fish, perhaps very similar to *Cladoselache*. This fish had already acquired the ability to submerge its primitive skeletogenous ectoderm and to develop from it the cartilaginous visceral skeleton and the trabecular components of the skull. This primitive gnathostome would have been provided with a fairly complete cavum cranii, contributed to largely by the otic capsules. It also, probably, had relatively complete nasal capsules, and fairly certainly a fenestrated sphenoidal region between the two pairs of capsules. It was also endowed with the power to build dermal scales and scutes.

This implies that its varying descendants should all have been able to form a bony exoskeleton. Some, however, did not do so; these constituted the Plagiostomi, and it is highly probable that the recent plagiostomes more nearly resemble this common ancestor than any of the other fishes.

Amongst the descendants which retained and improved on the power to form an exoskeleton the Teleostomi are the most outstanding. They early developed this exoskeleton on the head and it soon became attached to the cartilaginous skull. They also developed scutes along the edges of the lips and these became attached to the labial cartilages to form the labial bones. Those cartilages being to a large extent anchored by their muscular and fibrous attachments were, at first, also anchored to the dermal scutes of the side of the cheek, and only later gained mobility as we observe them in the modern Teleostei.

Whilst sharing with the teleosts the improved ability to form an exoskeleton and later cranial endoskeleton of membranous origin, the Chondrostei retained more of the original parental characters and failed to perfect the utilization of the skeleton-forming power.

If, as appears probable, the Holocephali are closely allied to the group from which the Tetrapods have been derived, it must be assumed that the recent Holocephali are to the parent stock much as the Polyodontidae are to the Acipenseridae, that is to say, they are degenerate in that they have lost the power to develop the exoskeleton which preceded the endoskeleton, which power was possessed by some of the Carboniferous members of the group. It may be that some such form as *Menaspis* is really nearer the stem of the Tetrapods than are the rest of the Holocephali.

Consideration of the geological antiquity of three of the four groups, and of the variety of the selachians in early Mesozoic and late Palaeozoic times, supports the view here taken that the details of the ancestry of the fishes are still wrapped in the mysterious depths of the late Palaeozoic rocks.

One alone of the four groups is so recent as to make its first appearance in later Mesozoic times, the Chondrostei.

From what little we know of them, it is probable that Pleuropterygii present the nearest approach to the primitive gnathostome at present available to us and, it may be remarked, it was undoubtedly an Elasmobranch. It further appears probable that not only the four recent groups, but also the Acanthodei and the Ichthytomi, should be regarded as illustrating different lines of variation among the descendants.

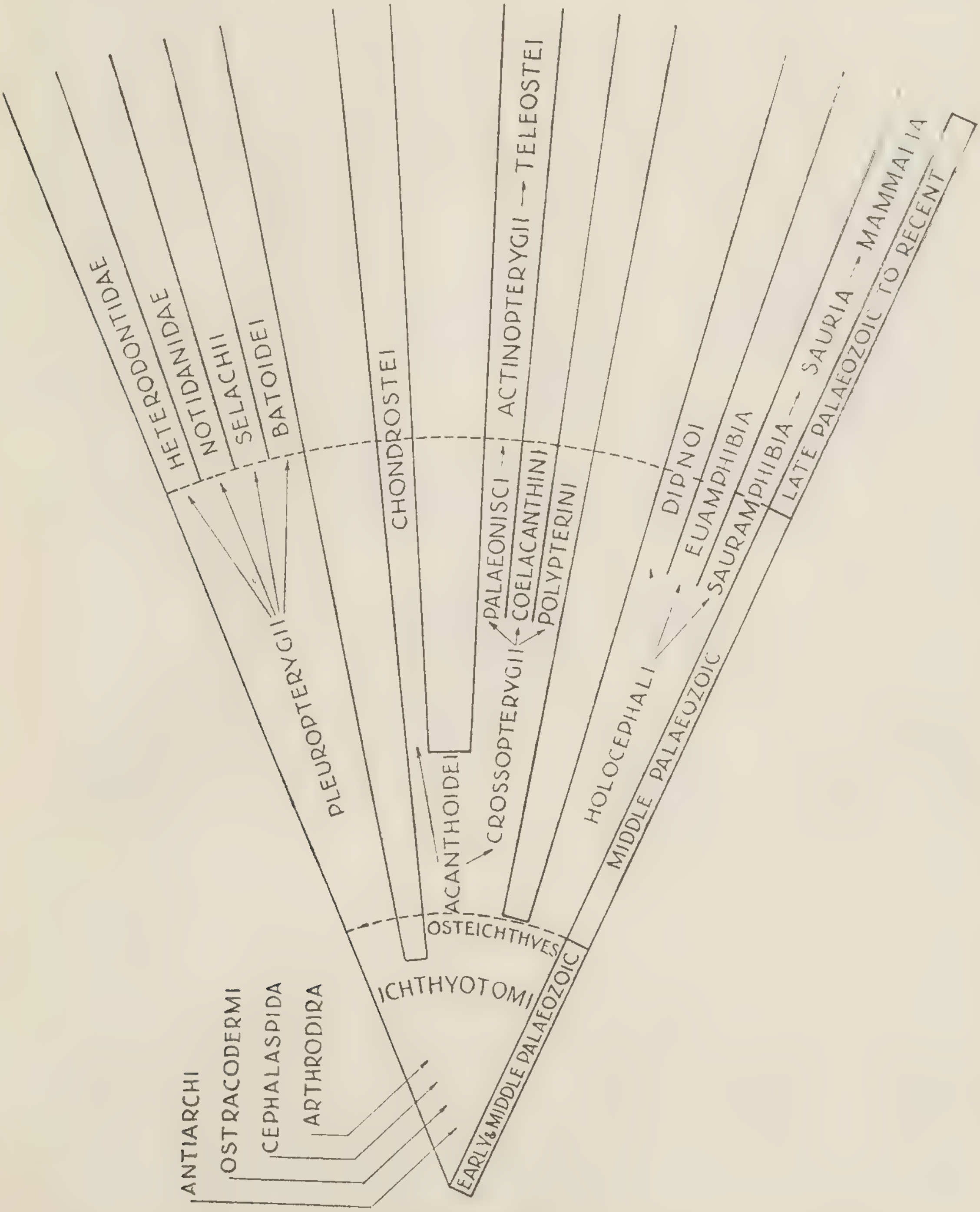

HETERODONTIDAE
NOTIDANIDAE
SELACHII
BATOIDEI
CHONDROSTEI
ACTINOPTERYGII → TELEOSTEI
PALAEONISCI
COELACANTHINI
POLYPTERINI
CROSSOPTERYGII
DIPNOI
EUAMPHIBIA
SAURAMPHIBIA → SAURIA → MAMMALIA
LATE PALAEOZOIC TO RECENT
PLEUROPTERYGII
ACANTHOIDEI
HOLOCEPHALI
MIDDLE PALAEOZOIC
OSTEICHTHYES
ICHTHYOTOMI
EARLY & MIDDLE PALAEOZOIC
ANTIARCHI
OSTRACODERMI
CEPHALASPIDA
ARTHRODIRA

Diagram II.

It is not improbable that, with increased knowledge of the Acanthodei, we shall find them to lie in the direct ancestry of the Chondrostei.

Watson (1925, p. 831), after offering a new reconstruction of *Chondrosteus*, wrote : " Thus such new information as I can add only emphasizes that resemblance between Chondrosteus and the Palaeoniscids which Traquair long ago pointed out, and shows how untenable is the view of Bridge, adopted by Swertzoff, that the Acipenseroides are the most primitive of the bony fishes and owe many of their peculiarities to a persistence of Elasmobranch structures." Even if Watson's belief that the post-orbital and maxilla in *Chondrosteus* " were immovably connected together " should prove correct, the most this would justify us in concluding would be that *Chondrosteus* is probably not an acipenserid. Clearly Watson is in error in concluding that evidence which indicates that *Chondrosteus* is dissimilar to the acipenserids is to be regarded as having any bearing on the origin of the latter forms.

Of the several groups, the Acanthodei, Chondrostei, Teleostomi, and probably the earlier Holocephali, all possessed pericranial ossifications and dermal scales and scutes, and there is in the arrangement of these ossifications a basic pattern which is reproduced in every group, or in forms which may be regarded as probably descended from the group.

The whole of the fishes and the amphibians possess in common a large synpterygoid covering, the basis cranii, excepting only *Eusthenopteron* and the embolomerous amphibians. Further, throughout the whole of these two classes we find the same pattern in the covering bones on the dorsum of the skull, namely, paired parietals, frontals, nasals, and premaxillae. This pattern, though departed from in individual instances, is so constant in occurrence as to indicate assuredly that it must be regarded as a common inheritance (Goodrich, 1930, pp. 285 *et seq.*).

These last considerations might be interpreted as indicating for the bone-forming fishes an ancestry different from that of the Plagiostomi, but it is impossible to disregard the undoubted elasmobranch characters of the Chondrostei and Acanthodei, or the teleostean and amphibian characters of the Holocephali.

The explanation of the conflicting evidence appears to be that all evolved from a common ancestral stock which possessed in varying degrees the inherited potential to develop bones and to develop them in accord with an already established basic plan.

I have attempted to convey these ideas on the evolution of the fishes in diagrammatic form.

It may be remarked that the above diagrammatic presentation (Diagram II) differs from that of 1931, wherein I represented the Dipnoi and Crossopterygii as being derived from a common stock which itself had been evolved from a preceding " Ganoid Stock ".

This changed attitude appears to me called for by the structure of the Holocephali, or by so much of the cephalic anatomy of these fishes as indicates a tendency towards the evolution of the amphibians. Regarding these features as the expression of an hereditary potential which culminated in the development of these Tetrapods, as I do, I am naturally led to conclude that the Amphibia have been evolved without any teleostome phase in their ancestry. Another fact that contributes towards the attitude taken is the discovery that the maxillae of *Polypterus* and its congeners are labial bones, and not, as I then believed, following Allis, truly homologous with the bones of the upper jaw of the Tetrapods.

PART II. THE AMPHIBIA.

The Cephalic Muscles of Branchiate Amphibians: 1. The Dipnoi; 2. The Anuran Tadpole; 3. The Urodele Larva; 4. The Perennibranchiate Urodele; 5. Review.

The Cephalic Muscles of the Abranchiate Amphibians: 1. The Adult Caducibranchiate Urodeles; 2. The Adult Anura; 3. The Adult Caecilians; 4. Review; Appendix. The Laryngeal Muscles of the Amphibians.

The Skulls of the Amphibians: 1. The Skull of *Neoceratodus*; 2. The Skull in the Euamphibia; 3. The Skull in the Embolomeri.

The Origin of the Amphibia: 1. General considerations; 2. The Evidence of the Cephalic Muscles on the Phylogeny of the Amphibia; 3. The Serial Homology of certain of the Bones in the Skulls of the Amphibia, and their bearing on the Evolution of the Class.

THE CEPHALIC MUSCLES OF BRANCHIATE AMPHIBIANS.

INTRODUCTION.

The inclusion of the Dipnoi amongst the Amphibia and their discussion in this section of the work is in accord with the conclusions arrived at as a result of reviews of their anatomy and embryology published by myself elsewhere (Kesteven, 1931*a*, 1931*b* and 1941). Those conclusions were that the Dipnoi are the most primitive amphibians known. Therefore, since they may be regarded as the most primitive members of the group which next falls for description and discussion, they are dealt with first.

The nomenclature of the muscles will continue, as far as possible, to reflect the conclusions arrived at relative to their homologies throughout the vertebrate series. It may here be explained that throughout the whole of this work it has been my practice to become completely familiar with the musculature of each group before commencing the study of the next higher group. Thus, the musculature of the branchiate Amphibia was studied before any of the abranchiate forms were examined at all. The object was to avoid the possibility of interpreting the musculature of the lower groups in terms of the higher. This has involved the use of provisional nomenclature until the whole of the work was completed, and its alteration, where required, on the completion of the work. The revision of the typescript which was entailed by this policy has permitted the inclusion in a few places of paragraphs such as this and others which include references to observations made during later portions of the work.

The use of the designation "pterygoideus" for one of the muscles of mastication in the fishes is an example in illustration of substitution of a name conveying an intimation of the final conclusion arrived at and introduced only after the work on the Reptilia was completed.

There is, however, a limit to which this policy of introducing the final conclusion into the nomenclature may be carried. For instance, it is believed that the anterior belly of the M. digastricus was derived from the Csv.1b, the M. intermandibularis, but it would, clearly, be inadvisable to apply such a designation to a flat sheet of muscle fasciculi.

The Table of Homologies is introduced to bring the work up to date, as it were, and it is introduced at the beginning with a view to presenting the conclusions of the section on the Amphibia as an introduction indicating the trend of the work.

LIST OF ABBREVIATIONS USED ON FIGURES 70–99.

A.c., Arytenoid cartilage; A.hy., M. abdomino-hyoideus; At.sc., M. attrahens scapulae; Br. 1 & 2, Branchial cartilages; Br.cl., Branchial cleft; C.he. & C.hy.e., M. interhyoideus; C.hy., Ceratohyoid cartilage; C.hy.a., M. ceratohyoideus anterior; Co., M. claviculo-branchialis; Co.hy.br., M. claviculo-hyoideus; C.p. & C.ph., M. constrictor pharyngei; Csd., Superficial dorsal constrictors; Csv.1a, M. submentalis; Csv.1b, M. intermandibularis; Csv.2a & 2b, Anterior and posterior parts of the M. interhyoideus; Cu., M. cucullaris; Dep.mn., M. depressor mandibulae; D.hy., M. dilator hyoidei; D.l. & D.lh., M. dorso-laryngeus; D.la., M. dilator laryngei; D.l.s., M. depressor labii superioris; E.br., The base of the external branchiae; Ep., Epithelium of the buccal mucosa; F.pr., Foramen prooticum; G.gl., M. genioglossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.gl.a., M. hyoglossus anterior; Hy.ph., M. hyopharyngeus; I.br., Mm. interbranchiales; I.h. & I.hy., M. interhyoideus; I.l.c., Inferior labial cartilage; I.sp., M. infraspinatus; L.a.b., Mm. levatores arcuum branchialium; L.br., The dorsal superficial branchial constrictor muscle: L.d., M. latissimus dorsi; L.hy., M. levator hyoidei; L.sc.i., M. levator scapulae inferior; L.sc.s., M. levator scapulae superior; L.v., M. laryngeus ventralis; Mas., M. massetericus; M.c. & Mk., Meckel's cartilage; Mm., Mm. interbranchiales; O-a-hy., M. omo-abdomino-hyoideus; Omo., M. omohyoideus; P.c., Pars cephalognathica; Pet.p., M. petro-hyoideus posterior; P.h.o., Posthyoid ossicle; P.n., Pars notognathica; Pr., Procoracoid; Pr.m., Processus muscularis; Pt., M. pterygoideus; Pt.a. & Pt.p., Anterior and posterior parts of the M. pterygoideus; Q-m., M. quadrato mandibularis; Qu., Os quadratum; R.ab., M. rectus abdominis; Rh.a., M. rhomboideus anterior; S.a.o. & S.a.ob., M. subarcualis obliquus; S.a.r., M. subarcualis rectus; S.a.t., M. subarcualis transversus; Sc., The scapula; S.c-t., M. spino-capitis transversus; S.l.c., Superior labial cartilage; Sph., M. sphincter laryngei; St.hy., Ceratohyoid cartilage; T., M. temporalis; V.mn., The mandibular ramus of the Vth nerve.

1. The Dipnoi.

THE CEPHALIC MUSCLES OF NEOCERATODUS FORSTERI.

(Figs. 70–73.)

(*a*) MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1b (Fig. 70).—This is the only representative of the Csv.1 sheet; there is no trace of a Csv.1a. The muscle arises from the greater part of the medial surface of the mandible and is inserted into the relatively broad mid-ventral raphe. Although not extensive superficially, the muscle is really massive, for the surface of the mandible is fairly deep. The mid-ventral raphe is a very strong membrane and the fibres are inserted onto its ventral surface.

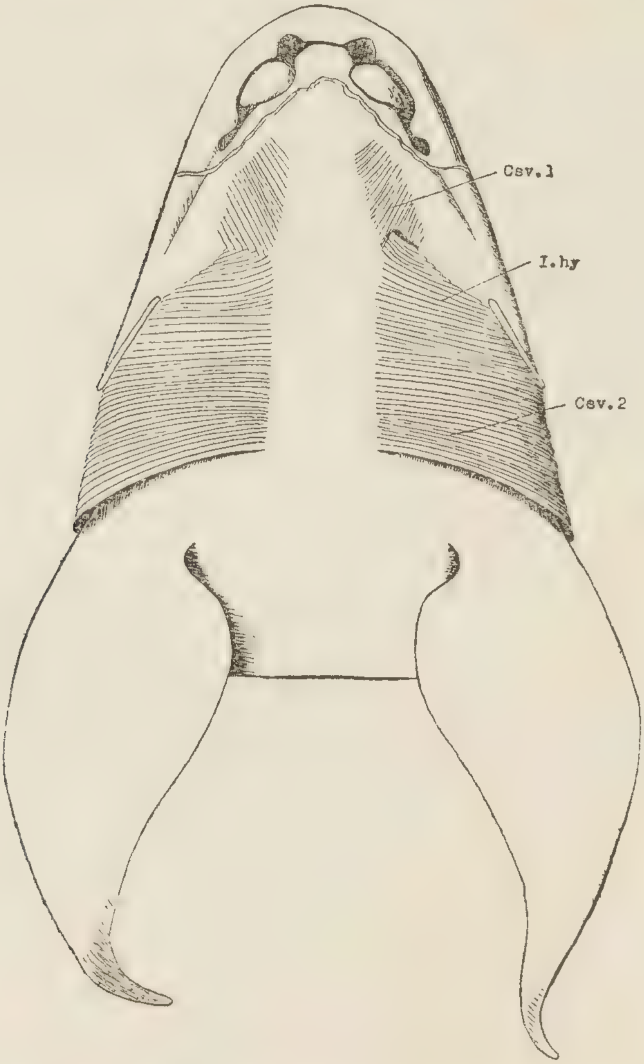


Fig. 70.—*Neoceratodus.* Ventral view of the superficial constrictors.

The posterior fasciculi of this muscle lie superficially to the most anterior portion of the M. interhyoideus to the extent indicated on the right side of Fig. 75, where the Csv.1b fibres have been cut away to show the underlying Cpr.2. There is a clean plane of separation between the two muscles and their separation is rendered the more easy by the different direction of their two sets of fasciculi.

Innervation.—The only nerve found to give fibres to the Csv.1b was the posterior myloid nerve (Nv.my.1).

TABLE OF PROBABLE MUSCLE HOMOLOGIES.

Serial Designation.	Particular Designations.*						
	Selachians.	Holocephali.	Teleosts.	Dipnoi.	Urodeles.	Anura.	Caecillians (Apoda).
Csv.1a and Csv.1b	Submentalis. Pars intermandibularis	Protr. inf. lab. inf. and Intermandibularis	Submentalis and Intermandibularis	Intermandibularis	Submentalis and Intermandibularis	Submentalis and Intermandibularis	Intermandibularis
Csv.1b²	Pars extra-mandibularis	+	Protractor hyoidei (in part)	O	O	O	O
Pterygoideus	Levator labii superioris	+	+	+	+	+	+
Quadrato-mandibularis	+	+	Temporalis	+	Temporalis and Massetericus	Temporalis and Massetericus major, minor and minima	Temporalis and Massetericus
Levator maxillae superioris	+	Levator labii superioris (?)	Levator arcus palatini	O	O	O	Levator quadrati
Cd.1.pr.	+	O	O	O	O	O	O
Csd.2a	+	+	Hyohyoideus (upper part)	+	Depressor mandibulae Pars notognathica	Pars notognathica	Pars notognathica
Csd.2b	+	Dilator operculi	Hyohyoideus (upper part)	+	Pars notognathica	Pars notognathica	Pars notognathica
Cd.2.pr.	+	Depressor mandibulae	Hyohyoideus (upper part)	Retractor mandibulae	Depressor mandibulae, Pars cephalognathica	Pars cephalognathica	Pars cephalognathica
Levator hyoidei	+	O	Add. arcus palatini Add. hyomandibularis Add. operculi	+	Pars cephalognathica	+ in tadpoles O in adults	?
Cv.2.pr. or Interhyoideus	Interhyoideus	Interhyoideus	Protractor hyoidei (posterior part)	+	Cerato-hyoideus externus	+	+
Csv.2a	+	+	Hyohyoideus (anterior part)	+	+	O	+
Csv.2b	+	+	Hyohyoideus (anterior part)	+	+	O	+
Csd.3 to 6	+	O	O	O	+	+	?
Csv.3 to 6	+	O	O	O	O	?	O
C.pr. 3 to 6 Interbranchiales	+	+	O	+	+	+	?
Levatores arcuum branchialium	+	+	+	+	One present in one species, otherwise O	O	?
Epiarcualia obliqui	+	+	Epiarcualia recti, obliqui and transversi	O	O	O	O
Adductores arcuum branchialium	+	+	+	O	O	O	O
Ventral branchial muscles	O	O	Subarcualia recti, obliqui and transversi	Subarcualia recti, obliqui and transversi	Subarcualia recti, obliqui and transversi†	Subarcualia recti, obliqui and transversi†	Subarcualia recti
Coraco-branchiales	+	+	Claviculo-branchialis	+	?	+ (one slip only)	?
Coraco-mandibularis	+	+	O	+	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis	Genio-hyoideus Genio-glossus Hyo-glossus Hyo-abdominis
Coraco-hyoideus	+	+	Claviculo-hyoideus	+			

* The + sign indicates that the muscle is present and that the serial designation has also been used as the particular. The O sign indicates that the muscle is probably absent.

† These muscles become the Petrohyoid, Dorsolaryngeus and Constrictor pharyngei muscles in the adult.

The mandibular adductors are very similar in all three Dipnoans. In addition to the two adductors of the lower jaws there are, in the Dipneumona, small retractores anguli oris, which Edgeworth (1926) describes as being developed from the adductor portion of the mandibular myotome. These are not present in *Neoceratodus*.

There are two main divisions of the mandibular adductor muscle mass, an internal and an external. Edgeworth (1911) followed Jacquet in designating the internal "temporal", and the external "pterygoid". These designations of Jacquet were most unfortunate, for it will appear later that it is the internal which is homologous with the pterygoid of the fishes and amphibians, whilst the external is homologous with the quadrato-mandibularis of the fishes.

THE PTERYGOIDEUS MUSCLE.

This takes origin from that part of the dorsum of the skull which is covered by the post-frontal bone (Kesteven, 1931*b*) and from the deep surface of that bone itself. It is a large nearly quadrilateral muscle with its antero-lateral and deep corner drawn out into a very strong short tendon which is inserted on to the upper edge of the lower jaw bone internal to the insertion of the quadrato-mandibularis. The tendon of insertion spreads out fanwise above, in the middle of the thickness of the muscle, so that the fasciculi arising from the skull are inserted into its deep surface and those from the post-frontal into its superficial surface. For a short distance above the insertion this tendon forms a sheath on the lateral surface of the muscle, separating it from the quadrato-mandibularis.

THE QUADRATO-MANDIBULARIS.

This takes origin from that area of the dorsum of the skull which is covered by the squamosal bone and from the deep surface of the squamosal, as well as from the anterior, free, surface of the descending process of that bone. This muscle also has a central tendinous sheet into which all the fibres, except those arising from the descending process of the squamosal, are inserted. As in the Pterygoideus, the sheet terminates anteriorly and inferiorly in a strong tendon which is inserted into the upper edge of the lower jaw bone. This insertion extends from the posterior edge of the teeth to just in front of the joint. The insertion of the Pterygoideus is medial to only the anterior half of this. The fibres arising from the descending process of the squamosal are inserted into a similar but much smaller tendon of their own, but this latter is completely fused with the other before its insertion.

Adams (1919) regarded these fibres arising from the descending process as a "masseter slip (adm.2)". I find that the division I have described is much more in conformity with the division of the adductor mass itself. The division between the small posterior mass is much more incomplete than the other and there is no structure intervening between those two portions. On the other hand, the division I have described is much more complete, fusion only taking place between the short deep fibres of the two divisions just above the insertions. Those insertions are placed one internal to the other, and they are separable right down to the bone without the severance of any fibres or fasciculi. Finally, the maxillary and mandibular divisions of the fifth nerve, after issuing from the foramen prooticum externum, pass forward and ventrad between these two divisions, thus delimiting the primitive quadrato-mandibularis from the pterygoideus, exactly as was found in the fishes.

Edgeworth's (1926) description and illustration of these muscles and the related divisions of the Vth nerve are a little misleading. Actually, however, the discrepancy is only apparent. In the adult the origin of the quadrato-mandibularis, levator mandibulae posterior of Edgeworth, extends dorsad and mediad so that the proximal portion of the mandibular division of the nerve comes to lie internal to this muscle.

The use of the designation "levator" for this muscle, whilst mechanically correct, is, from the point of view of muscle homologies, quite wrong.

The two muscles of mastication are separated by an interval filled by loose fascial tissue, and, in their anterior portions, by the emerging second and third branches of the fifth nerve which lie in this tissue.

The fifth nerve presents the same relations to these two divisions of the muscles of mastication as was found in the fishes. The second and third emerge from the prootic foramen together and lie at once between the Mm. pterygoideus and quadrato-mandibularis. The nerve to the former muscle arises from the main division of the mandibular branch immediately outside the foramen and turns dorsad medially to the maxillary branch. The nerves to the latter muscle, two in number, leave the main branch a little later and reach the muscle laterally to the maxillary branch. The terminal myloid branch reaches the surface of the muscles close to their two tendinous ends, and immediately turns laterad and then caudad around the lateral surface of the M. quadrato-mandibularis tendon to reach the mandibular foramen. Immediately within the foramen it is joined by the mandibular branch of the seventh nerve, the chorda tympani, but does not fuse with it until the posterior myloid nerve to the Csv.1b has been given off (Fig. 72). The anterior myloid nerve (Nv.my.) gives off one more branch before itself emerging from the canal far forward.

(*b*) THE MUSCLES OF THE HYOID SEGMENT.

The Csv.2 and the Csd.2 are quite continuous posteriorly (Fig. 71). The origin of the Csd.2 is from the dorsal fascia just a little dorsally to the line of attachment of the opercular membrane. The posterior margin of the muscle is the free edge of the membrane. The insertion is per medium of the Csv.2 into the mid-ventral raphe. The continuity of the two portions of the sheet is interrupted in the region of the operculum and the suboperculum by two lines of insertion on to the deep surface of those bones. The antero-dorsal portion thus delimited is, apparently, homologous with the M. levator operculi of the bony fishes. The insertion of the fasciculi of this muscle is along a line a short distance below the dorsal margin of the deep surface of the operculum. A little distance below this line a second small sheet of fasciculi arises; these are inserted on to the deep surface of the suboperculum, and below them the Csv.2 takes its origin from the same surface.

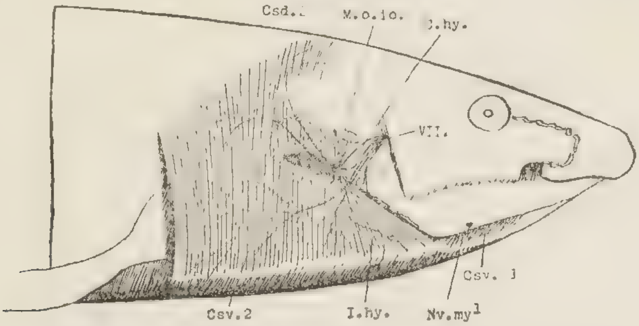


Fig. 71.—*Neoceratodus*. Lateral view of the superficial constrictors.

In addition to these small muscles beneath the opercular bones there is a small but remarkably massive muscle which arises from an oval area of the deep surface of the operculum infero-anteriorly. The fasciculi are all gathered to a short stout tendon which is inserted on to the upper edge of the deep surface of the suboperculum at its anterior end.

The Cpr.2, M. interhyoideus, is very similar to that muscle in the Elasmobranchia. It arises from a small area on the lateral surface of the ceratohyoid just behind the angle of the jaw and deep to the mandibulo-subopercular ligament. Its anterior fasciculi run forward at a sharp angle, the posterior fasciculi run directly transversely, those in between having intermediate directions. The muscle lies in the same plane as, and is inseparable from, the anterior fasciculi of the Csv.2. The most anterior fasciculi are inserted deep to the posterior fibres of the Csv.1.

These hyoid muscles are, of course, innervated by the motor twigs of the facial nerve. The location of these twigs over the surface of the muscles is shown in Fig. 71.

The seventh nerve gives off the palatine branch whilst it is within the facial canal. This palatine canal leaves the other a short distance from the cranial end and passes directly ventrad; just before it reaches the ventral surface, the canal turns rostrad and mediad and runs forward for a short distance within the cartilage and then reaches the surface of the cartilage so that the nerve lies in a parabasal canal whose walls and roof are cartilaginous and whose floor is supplied by the parasphenoid bone.

Continuing dorso-laterally with a slight caudal inclination, the ramus hyomandibularis issues from its canal between the otic and basal roots of the quadrate, as previously described

(Kesteven 1931*b*). Almost at once the nerve breaks into three branches. The first leaves the anterior side of the nerve, runs laterad and rostrad behind the otic root and ramus of the quadrate for a short distance and then, turning rostrad, plunges into a canal which tunnels the ramus of the quadrate, a short distance above the articular head, in a direction ventrad and rostrad. The nerve issues from this canal under those fibres of the M. quadrato-mandibularis which arise from the front of the quadrate. If these fibres be pulled inward, without disrupting their attachment, the nerve is brought into view as it runs forward along the lateral edge of the muscle to reach the myloid foramen in the mandible. A short distance within that canal, just beyond the departure of the posterior myloid nerve, this branch of the facial fuses with the myloid branch of the fifth nerve. This has been identified as the Chorda tympani (Nv.ch-t., Fig. 71).

The next branch of the hyomandibular trunk is the lateralis component. This leaves the anterior side of the main nerve and enters, almost immediately, the lateral line canal which lies nearly parallel with the posterior margin of the quadrate and anterior margin of the operculum.

A second inferior mandibular branch next leaves the same side of the main nerve and runs ventrad, laterad and rostrad, deep to the anterior margin of the operculum, then deep to the mandibulo-subopercular ligament and forward along the medial edge of the ventral surface of the mandible for a little distance. This probably communicates with the posterior myloid nerve, but the communicating twig was not found.

The hyomandibular nerve now breaks up into its several motor twigs to the hyoid muscles, whose distribution is shown in Fig. 76.

There is no reason to doubt the complete homology of the two superficial constrictor sheets, Csv.1b and Csv.2, with the first and second sheets in the fishes. One should, however, note that in *Ceratodus* the resemblance of the hyoid sheet is to the Selachians and Holocephali rather than to the bony fishes. In these latter the hyoid constrictor runs dorsad under cover of the opercular components, whilst in the dipnoan the sheet is, in its posterior portion, quite superficial. It is true that in *Ceratodus*, as in the teleosts, the anterior portion of the dorsal constrictor lies beneath the opercular bones, and it would appear that in the bony fishes the more complete bony equipment of the opercular flap had invaded the muscular sheet, but that the development of the branchiostegal membrane had captured the sheet whilst the opercular skeleton had grown backward in a fold superficial to that membrane. It is probable that the branchiostegal rays are really superficial to the muscle sheet in all the fishes. They are obviously so in the eels.

In *Neoceratodus* there is no branchiostegal membrane, the opercular skeleton is but poorly developed, and the conditions generally are as in the Holocephali.

Edgeworth (1911, p. 188) says that " In Ceratodus the myotome of the mandibular segment spreads upwards lateral to the Gasserian ganglion and separates from the lateral half of the intermandibularis . . . It divides into outer and inner portions . . . the former of which . . . arises from the trabecular wall and the latter from the outer and anterior surface of the quadrate. The intermandibularis joins its fellow in a median raphe and becomes attached laterally to Meckel's cartilage ; its posterior end extending backwards underlies the fore part of the interhyoideus ", and (p. 212) " The hyoid myotome and the interhyoideus spread backward in the opercular fold and form . . . anteriorly a levator hyoidei inserted into the upper end of the hyoid bar, and an interhyoideus, and posteriorly a continuous ventro-dorsal . . . sheet in the operculum . . . the anlage of the hyomaxillaris ligament is cut off from the upper edge of the interhyoideus and spreads forwards to the hind edge of Meckel's cartilage."

His description of the arrangement of the hyoid muscles in a 55 mm. specimen of *Protopterus* is also of interest here (Edgeworth, 1926, p. 724). " The levator hyoidei is inserted into the knee of the hyoid bar . . . The most posterior fibres of the constrictor hyoideus form a continuous dorso-ventral sheet, but the majority have separated into three portions—dorsal, middle and ventral. The dorsal portion passes from the auditory capsule to the operculum, the middle portion from the operculum to the suboperculum, and the ventral from the suboperculum to the mid-ventral line. The middle portion has extended forwards, and its anterior portion forms a separate muscle, the retractor mandibulae, of horizontal fibres easily distinguishable from the vertical fibres of the constrictor. The dorsal edge of the retractor rises and, in front of the dorsal portion of the constrictor, is attached to the auditory capsule. The posterior end of the retractor is attached to the operculum and suboperculum. The muscle extends forward in front of the hyoid bar and is inserted into the hind end of the jaw to the splenial and angular bones. The anterior edge of the ventral portion of the constrictor is slightly separated from, and overlaps, the hind edge of the interhyoideus."

Comparing these descriptions with the muscles in the adult *Neoceratodus*, we note that the levator hyoidei of the larval form is no longer present and that there is now no recognizable overlap between the contiguous edges of Csv.1 and Csv.2, but that they are indistinguishably blended. There is, however, a very close resemblance between the hyoid sheets in the adult *Neoceratodus* and the 55 mm. *Protopterus*, more particularly in the division of the upper end of the sheet beneath the opercular bones.

In front of this point in the adult *Neoceratodus* we find a muscle, which is essentially similar to the interhyoideus of the selachians, situated deep to the fore end of the superficial hyoid constrictor and to the posterior end of the intermandibularis.

It would appear from Edgeworth's Figure 19 that the overlap of the anterior portion of the interhyoideus beyond the posterior margin of the intermandibularis, in the 19 mm. *Protopterus*, is dorsal to that muscle.

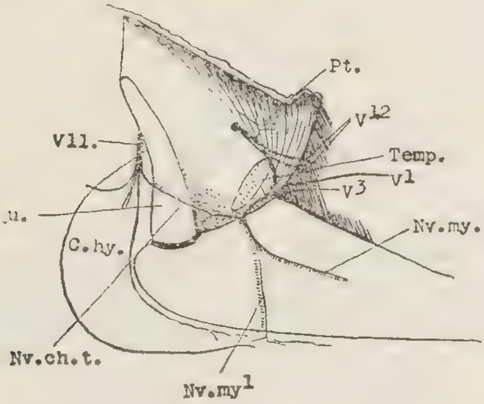


Fig. 72.—*Neoceratodus.* Semi-schematic presentation of some of the branches of the Vth and VIIth nerves. C.hy., Ceratohyoid; Nv.ch-t., Communicating branch of the VIIth to the myloid branch of the Vth; Nv.my., Myloid nerve; Nv.my^1., Posterior myloid nerve; Temp., Tendon of the tempo-masseteric muscle.

If this be so, then we may conclude that it is the anterior portion of the hyoid constrictor sheet which persists as the interhyoideus in the adult *Neoceratodus*. It also seems not unreasonable to assume, for the present, that the antero-posteriorly directed lateral fibres of the interhyoideus are homologous with the retractor mandibulae of the *Protopterus*.

Edgeworth (1926, p. 724) remarks that Rudge was of the opinion that the retractor mandibulae of the Dipneumona was homologous with that portion of the Csd.2 which Lightoller has since designated the pars quadrato-hyoidea. With this opinion Edgeworth is unable to agree. He points out that a pars quadrato-hyoidea is not present in the dipneumonous lungfishes, and that the retractor results from a relatively late forward growth from the middle portion of Csd.2.

To the present writer it appears that both the abortive muscle of *Neoceratodus* and the fully developed retractor of the Dipneumona are to be compared with the hyoid component of the retractor hyoidei of the bony fishes, the whole of the deep sheet to be regarded as homologous with the interhyoideus of the elasmobranchs, but presenting a partial modification and specialization. A deep intermandibular fascia which is present in *Neoceratodus* may be actually the homologue of the anterior portion of the protractor hyoidei. Unfortunately we do not know the later development, but if it be a forward extension of the "hyomaxillaris ligament" of Edgeworth then it is developed in a manner very similar to the protractor hyoidei of the bony fishes.

I have been able to dissect specimens of *Lepidosiren* measuring 48 to 50 mm. These, which I have to thank Professor W. E. Agar for, are young which have just completed the metamorphosis, and their muscular anatomy must be essentially similar to that of the adults.

The retractor mandibulae is an obvious little muscle lying along the outer edge of the skull, along the surface of the squamosal bone. There can be little doubt that it is completely homologous with the pars cephalognathica of the depressor mandibulae of the whole of the amphibians and reptiles. The homology of this muscle is discussed later, and it is regarded as the modified form of the pars epihyoidea.

(c) BRANCHIAL MUSCLES (Fig. 73).

Musculi Marginales. Interbranchial Muscles.

Cpr. 3, 4, 5 and 6.—Each of these has a fleshy origin from the under side of the cartilaginous roof of the gills near the lateral margin. From this origin each muscle passes almost vertically downward but with a curve first outward and then back medially. Where they take origin, the fasciculi of each muscle are gathered together to produce an oval fleshy belly, but on entering the interbranchial septum they are separated and spread out to form a thin layer immediately beneath the anterior gill filaments. As they are followed downward it is found that they spread steadily to form a slowly widening ribbon, then, a little more than two-thirds of the distance towards the inferior angle of the pouch, the muscle fibres quite suddenly give place to fine tendinous fibres which are continued to the inferior margin of the septum.

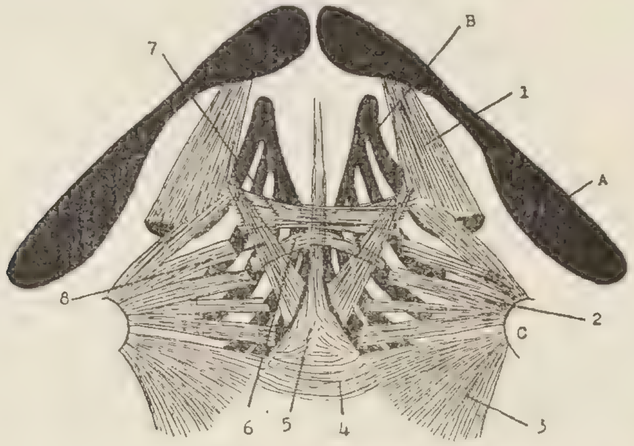


Fig. 73.—*Neoceratodus.* A semi-schematic presentation of the ventral branchial muscles, as seen from below. 1, M. subarcualis rectus; 2, The five Mm. coracobranchiales; 3, M. cucullaris; 4, M. sphincter oesophagi; 5, M. subarcualis transversus V; 6, M. subarcualis transversus III; 7, Mm. subarcuales transversi I and II; 8, Mm. subarcuales II-V; A, Hyoid arch; B, Branchial arches; C, The coracoid.

There is no seventh deep constrictor.

These muscles are designated constrictor branchiales by Edgeworth in his description of the development in *Protopterus* and *Lepidosiren* (1926, p. 727).

Their homology with the interbranchial muscles of the Selachii appears quite obvious, although they are no longer related to the superficial constrictors, these latter being absent. The resemblance to the interbranchial muscles of the Holocephali is very close. One observes that these dipnoan interbranchial muscles differ from those of the fishes in that they arise from the skull dorsally instead of from the upper elements of the branchial arches, extrabranchials or pharyngobranchials. On the other hand, it should be noted that this dorsal origin for these muscles is correlated with, and probably conditioned by the absence of the caudo-dorsal " return " direction of any part of the branchial arch skeleton dorsally. In the dipnoan the segments of the branchial arches are all in the same plane, so that a dorsal attachment for muscles external to them and in the same plane must of necessity be to skeletal or fascial structures dorsally.

We shall find essentially similar relations present in the anurous amphibian tadpoles.

It will be remembered that there are no interbranchial muscles developed in any of the bony fishes.

Levatores 3 to 7 (levatores arcuum branchialium) are very similar muscles. Each has a fleshy origin from the under surface of the temporal cartilaginous gill-roof just along the line where that merges with the side wall of the skull and otocrane. Each is a short, round muscle and its point of origin is directly above the point of its insertion into the dorsal end of the branchial arch, in front of and medial to the origin of the deep constrictor. The seventh is the longest of these muscles ; the fifth branchial arch is not fully developed and does not reach so far dorsally as the others.

The Cucullaris (Fig. 73) arises immediately behind the seventh levator arcuum by a strong tendinous band of fibres which " fans " out at once, and also from the antero-ventral surface of the post-temporal immediately behind the origin from the skull and at a slightly lower level. From this origin the fibres spread out and, passing ventrally and medially, gain insertion into scapular and suprascapular regions of the pectoral arch. Inferiorly it is impossible to separate this muscle from the fifth coraco-branchial muscle. The two together form a strong muscular wall for the fleshy portion of the posterior wall of the atrium. The condition recalls that described in *Dasyatis* (p. 46).

These branchial levators recall more strongly those of the selachian fishes than those of the teleosts. In the latter the levators are closely bunched together at their origin from the skull, whilst in the Dipnoi, for the dipneumonous forms are similar to *Neoceratodus*, they are spaced out, one behind the other in regular sequence, as in the Selachii.

The extensive cucullaris recalls that of the bony fishes in its development from a single branchial myotome. Greil (1908) described the muscle plate of the fifth branchial arch as developing into four muscles dorsally, of which the most posterior is that which he designated the " levator scapulae ". This is apparently the cucullaris of my description. So far as I am aware, the development of the cucullaris in the Dipneumona has not been observed, but Edgeworth (1926, p. 725) says of the larvae of *Protopterus* and *Lepidosiren* that " In the fifth arch there is a constrictor branchialis V which extends downwards through the arch and is continuous ventrally with the hinder part of the Coraco-branchialis V " and that in the 55 mm. specimen (of *Protopterus*) " Constrictor branchialis V and the corresponding portion of coraco-branchialis V have undergone a considerable extension backwards and form a broad sheet of dorso-ventral fibres, which arise from the back of the auditory capsule and, behind that, from the post-temporal bone which has now developed."

It is highly probable that later stages would reveal that this backward extension is the inception of the development of the cucullaris.

It would appear from Edgeworth's work (1911) that the cucullaris of the bony fishes is always developed from a single branchial muscle plate when present at all, but that in the Selachians (1911 and 1926*b*) the cucullaris is developed from small portions of the dorsal ends of several branchial muscle plates.

Whilst thus resembling the cucullaris of the bony fishes in its development, the muscle in the dipnoans, as observed in the adult, is more similar to that of the selachians. In the bony fishes the muscle is small and so closely resembles the levatores arcuum branchialium that it has been so designated by several writers. In the selachians it is an extensive muscle very similar to that of the dipnoans but, in the generality of instances, more massive.

(*d*) THE HYPOBRANCHIAL MUSCLES.

Subarcuales transversi (Fig. 73).—There are three of these. Numbers one and two arise together from the first two ceratobranchial cartilages and from a fibrous band between the two cartilages. The third arises from the third ceratobranchial. The three muscles incline toward one another at the mid-line and there form a continuous sheet immediately beneath the bases of the third and fourth ceratobranchial cartilages. There is no median tendinous raphe ; the fibres are in part continuous and in part interlace at the mid-line. According to Edgeworth, Jacquet designated these Mus. chiasmique. They are the second and third interbranchial muscles of Greil.

Constrictor pharyngei (Fig. 73).—Edgeworth tells us that this is developed from the fifth subarcualis transversus ; it is therefore included in this subsection, but the longitudinal fibres which enter so largely into its constitution suggest that there is also another component. The muscle arises from the median surface of the fifth ceratobranchial on each side, and forms a muscular layer to the floor of the pharynx between those cartilages. The posterior fibres pass transversely and either are continuous or interlace across the mid-line. The middle fibres bend forward and either interlace or are continued forward as two parallel, closely touching bundles of fasciculi which terminate in a common tendon ventral to the chiasmatic muscle. This tendon is inserted into the tough fibrous tissue in the floor of the mouth behind the hyoid copula.

Subarcuales recti.—Two pairs of recti are present, the posterior according to Edgeworth being composite muscles.

Subarcualis rectus 1 (hyo-branchialis) (Fig. 73) takes origin from the posterior face of the ceratohyoid near its median end. A stout fleshy muscle at its origin, it flattens out and broadens as it passes caudally and slightly laterally to be inserted on to the inferior edge of the first ceratobranchial along the middle third of its length.

Subarcuales recti 2, 3, 4 and 5 (Fig. 73) form one continuous ribbon of muscle which arises in front from the first ceratobranchial cartilage just medial to the median margin of the insertion of S.arc.r.1 and passes back beneath the other arches, being bound to each ceratobranchial as it passes below it, to be inserted on to the base of the fifth ceratobranchial cartilage.

The coraco-branchiales (Fig. 73).—These are five ribbon-like muscles which arise, one behind the other, from the middle of the length of the inferior surface of the ceratobranchial cartilage and converge to be inserted close together on to the coracoid portion of the pectoral arch at a little distance from the mid-line on each side. The last of these is much broader than the others, and, as already described, is inseparable from the lower and median margin of the cucullaris.

(e) THE HYPOBRANCHIAL SPINAL MUSCLES.

The Coraco-mandibularis (genio-hyoideus) arises behind from the coracoid arch on either side of the mid-line. It is a flat muscle and tapers to its insertion by a short ribbon of tendon into the symphysis.

The Claviculo-hyoideus is a massive tetrahedral muscle. The base of this tetrahedron is at its origin from the coracoid and from a membrane dorsal to the coracoid which is attached to the pectoral arch on each side. One of the sides of the muscle is exposed by the removal of the ventral constrictors and the coraco-mandibularis; the other two sides lie against the coraco-branchial muscles. The apex is inserted into the hyoid copula.

The Genio-hyoid ligament is a short, round ligament which binds the hyoid copula to the symphysis.

There remains for description a slender fleshy rounded muscle which arises from under the edge of the dorsal squame of the squamosal (Kesteven, 1931). At its origin it lies above the outer edge of the first gill septum, just lateral to the origin of Cpr.3, the first interbranchial muscle, near the lateral margin of the cartilaginous atrial roof. From this origin the muscle passes medially, forward and ventrally, to be inserted into the epibranchial cartilage of the first arch along with but posterior to the first levator arcuum branchialium.

Actually this muscle arises almost in continuity with the first branchial deep constrictor and is inserted almost in continuity with the first branchial levator. Since the levator is developed from the medial and dorsal portion of the general constrictor sheet, it appears that this should be regarded as an aberrant piece which was situated at the line of fission between the two derivatives and has remained attached to both. It was only found on one side of the specimen dissected.

From the deeper layer of the branchial muscle plates there are developed, in the selachians, epiarcual branchial muscles and interbranchial muscles, in the bony fishes, epiarcual branchial muscles and subarcual branchial muscles, and in the dipnoans epiarcual, interbranchial and subarcual branchial muscles.

It has been demonstrated that the interbranchial muscles of the selachians and the subarcual muscles of the bony fishes are both developed from the same ventro-median portion of the primordial muscle plate. Ontogenetically, therefore, these muscles are homologous and they have been so regarded in a previous section of this work. We have now to consider in what light we must view the interbranchial and subarcual muscles of the dipnoans.

It appears to the writer that, beyond question, the subarcual muscles in the Dipnoi and Teleostomi are completely homologous, and it might, therefore, appear to follow that the interbranchial muscles of the Selachii cannot also be homologous with the subarcual muscles of the Teleostomi. It would certainly appear that we must regard the primordial muscle plate in the bony fishes as having grown down and given rise to the subarcual muscles and as having become completely aborted between these and the epiarcual muscles, whilst in the Dipnoi the intervening portion has persisted and given rise, as in the Selachii, to the interbranchials.

A strict interpretation of the facts is perhaps as follows. The Dipnoans present a more primitive condition than the bony fishes; in them we are permitted to observe the intermediate stage in the evolution of the subarcual muscles. In this stage they arise as ventral extensions from the ventro-median portion of the deeper part of the primitive constrictor sheets. In the bony fishes a further stage has been arrived at. In this the connecting piece, which we designate the interbranchial muscle, has been lost.

If this be correct then, whilst there is ontogenetic evidence that the subarcual muscles are homologous with the interbranchials of the Selachians, phylogenetically the interbranchial muscles are homologous in the Dipnoi and the Selachians, as also are the subarcual muscles in the Dipnoi and the Teleostomi.

2. The Anuran Tadpoles.

(Figs. 74–78.)

The following description of the masticatory and branchial muscles of the anuran tadpoles is taken directly from dissections of the tadpole of *Mixophyes fasciolatus.* The illustrations are similarly derived. I was fortunate in the spring of 1932 to obtain a large number of these tadpoles and was able to rear them till some had acquired indubitable specific characters. They were of relatively large size, measuring 7 to 8 cm. in length, the heads being 1–5 cm. long and of equal width and only slightly less deep. I was able to dissect out most of the muscles after staining with picric acid and borax carmine. Doubtful points in the anatomy and innervation were checked or corrected by the study of thick lightly-stained sections rendered transparent by the Spalterholtz method. I have, moreover, made careful comparison with preparations of the smaller tadpoles of *Hyla aurea, H. cerulea, Crinia* sp.* and *Lymnodynastes* sp. The resemblance was so complete that no differences were observable. The primordial cranial and branchial structures were so similar one to another and to those of *Rana*, that one is justified in making the assumption that the description here given of these muscles may be accepted as being truly and completely one of the muscles of the anuran tadpoles generally.

The primordial cranium is so essentially similar to that of *Rana* that I have reproduced, only slightly modified, Gaupp's illustration thereof in illustration of that of *Myxophyes.* I have, however, preferred to designate the suprarostral cartilage " upper labial " and the infrarostral " lower labial " in order to convey their complete homology with the corresponding structures in the fishes.

The primordial visceral skeleton also is essentially similar to that of *Rana.* The hyoid, or first copula, is rather better developed and is articulated on each side to the anterior edge of the hyal cartilage. The two hyal cartilages are, as in *Rana*, broad and massive. They articulate one with the other in the mid-line, and on each side with the inferior edge of the muscular (antorbital) process. The second copula lies in contact with the median edges of the hyal cartilages in their posterior halves, these edges diverging to accommodate the copula. This second copula is a small quadrilateral plate which overlaps inferiorly the similarly shaped, but larger, planum hypobranchiale. This latter shows no division into right and left halves, as it does in *Rana.* The four branchial arches are articulated to the lateral margin of the hypobranchial plate much as in *Rana*, and have similarly serrated edges.

MIXOPHYES TADPOLE.

Stage A. (Figs. 74–76.)

The dimensions of this stage are those given above. There is as yet no sign of the development of either limb, and the lungs are but small, apparently functionless organs, for the little animals were observed not to swim to the surface for air as did those in which, at a later stage, the lungs were found to be much enlarged.

The Submentalis muscle (Csv.1a, Fig. 74) appears as a small nodular condensation of tissue which takes the picric acid stain well, and stands out quite clearly, immediately behind the symphysis of the inferior labial cartilages. As yet no definite muscle fibres are observable under the dissecting microscope.

The Intermandibularis muscle (Fig. 74, Csv.1b) is a very fine thin band of muscle fibres which arises on each side on the anterior and superior surface of Meckel's cartilage along the centre one-third of its length and passes round the lateral surface of the cartilage, and then passes caudally, ventrally and medially to be inserted with its antimere into a median ventral raphe.

---

* Of these I have had some hundreds for study, presenting in all forty-seven stages of development from ovum to adult form.

In situation this muscle encloses a triangular area whose third side is the posterior margin of the inferior labial cartilages. Where the fibres leave Meckel's cartilage the band of fibres lies in the horizontal plane, but as they pass medially the more posterior fibres come to occupy a position dorsad to the anterior fibres so that the median raphe is almost in the vertical plane.

Innervation.—Both these two muscles are innervated by the mandibular ramus of the Vth nerve. The actual innervating branch to the Csv.1b was quite plainly seen leaving the main nerve just as that passed across the outer surface of Meckel's cartilage. The nerve to the Csv.1a was found in stage C described later.

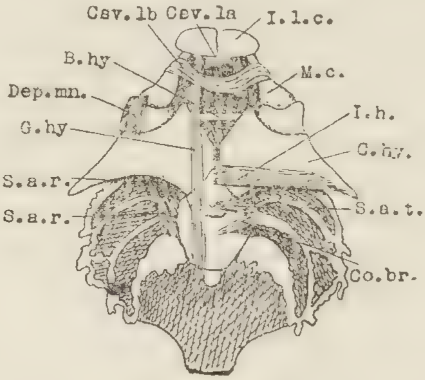


Fig. 74.—*Mixophyes* tadpole, stage A.—Ventral aspect.

The Interhyoideus muscle, Csv.2 (Fig. 74, I.h.), arises from the mid-ventral raphe and is inserted on each side on to the inferior, postero-lateral, corner of the hyoid cartilage. The muscle is fairly stout, oval in transverse section, and a certain number of the fasciculi cross the mid-line and arise amongst those of the opposite side.

Innervation.—The motor twig for this muscle leaves the hyomandibular ramus of the VIIth nerve after that has passed mediad and ventrad from between the two heads of the depressor mandibulae muscle.

The Dilator hyoidei muscle, Csd.2 (Figs. 75, 76, D.hy.), arises from the dorsal edge of the antorbital muscular process and passes caudad, laterad and ventrad across the external surface of the process, to be inserted into the ventral edge of the lateral margin of the hyoid cartilage immediately lateral to the joint with the process and in front of the origin of the interhyoideus muscle. The dilator hyoidei is a short, thick, relatively broad muscle and occupies practically the whole of the concave depression on the outer surface of the muscular process.

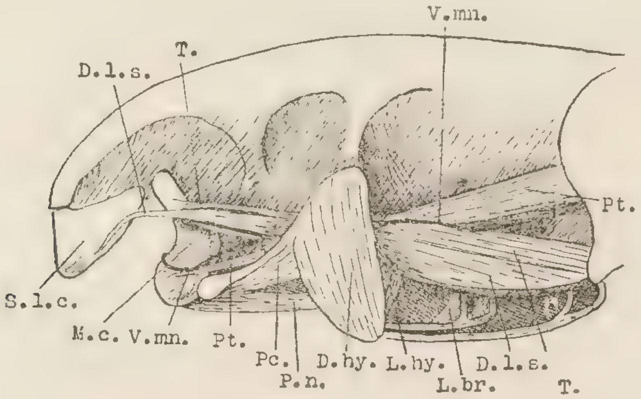


Fig. 75.—*Mixophyes* tadpole, stage A.—Lateral aspect.

Innervation.—The motor twig for this muscle leaves the hyomandibular trunk of the VIIth nerve before it passes beneath the depressor mandibulae muscle.

The Depressor Mandibulae muscle presents itself even in this early stage in the two portions which Lightoller has designated partes cephalognathica and notognathica. It must, however, be remarked that (though I have made use of those designations with a view to establishing their identity with the parts of the muscle in the adult frog) at this stage of its development the former is not entitled to its name, for it does not arise from the cranium but from the mandibulo-maxillary visceral skeleton.

The Pars Cephalognathica (Figs. 75, 76, P.c.) arises under cover of the dilator hyoidei, from the lower part of the outer surface of the muscular process.

The Pars Notognathica (Fig. 75, P.n.) arises from the lateral edge of the hyoid cartilage under cover of the anterior edge of the same muscle.

The two portions taper rapidly and are inserted by a short common tendon into a backward turned spur on the infero-lateral corner of Meckel's cartilage.

The contiguous edges of these portions are separated by a very narrow interval, and at their origins the joint between the process and the hyoid cartilage lies deep to the interval. The uppermost fibres of the pars cephalognathica have an inclination ventrad, the lowermost fibres of the pars notognathica an inclination dorsad, as they pass forward to their insertion.

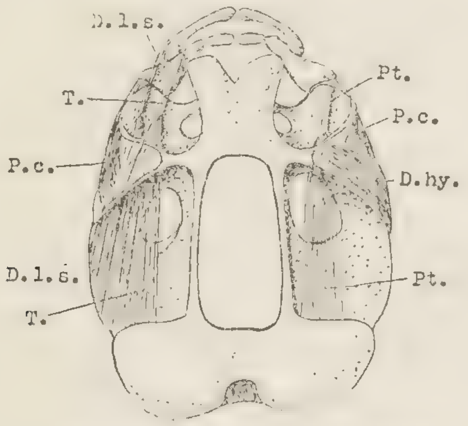


Fig. 76.—*Mixophyes* tadpole, stage A.—Dorsal aspect.

Innervation.—This is by twigs of the hyomandibular trunk of the VIIth nerve as it passes from beneath the dilator hyoidei muscle, that is to say, dorsally to it.

The mandibular adductor muscle mass presents five distinct components. Together they fill the space between the ethmoid region of the skull and the upturned antorbital muscular process, and, extending backward, cover the floor of the orbit. Although thus closely packed, they are quite readily dissected asunder.

The Depressor Labii Superioris Longus (Figs. 75, 76, D.l.s.) is an elongated ribbon of muscle fibres which takes origin from the outer margin of the floor of the orbit along its length. It tapers gradually as it extends forward and its fibres give place to a fine tendon as they reach the transverse level of Meckel's cartilage. The tendon is continued onward in the loose tissues of the side of the mouth and is inserted into the superior labial cartilage about the middle of its length, close to the inferior margin, whereon are set the horny larval teeth.

The Depressor Labii Superioris Brevis is a much shorter muscle which arises from the anterior edge of the muscular process and passes forward, covering the anterior end of the depressor longus to be inserted into the tendon of this latter muscle.

The Temporalis (Figs. 75, 76) arises from the floor of the orbit medially to the long depressor. As it extends forward it comes to lie ventrally to the anterior end of the long depressor. Like the other muscles, it tapers to a fine, but short, tendon which is inserted into the superior surface of Meckel's cartilage about the junction of the posterior and middle thirds of its length.

The Pterygoideus Muscle (Figs. 75, 76) is similar in shape to the temporalis. It arises from the cranial wall and orbital floor medially to the suborbital vacuity. It passes forward across the antorbital bar beneath the other three muscles and is inserted into the upper surface of Meckel's cartilage behind the temporalis.

The Massetericus is a very thin sheet of short muscle fibres which arise from the medial surface of the muscular process close to the anterior edge thereof and passes cephalad, ventrad and slightly laterad, to be inserted into the proximal end of Meckel's cartilage just in front of the insertion of the pterygoideus.

Innervation.—All these muscles of mastication are innervated by twigs from the mandibular ramus of the Vth nerve as it passes them.

The mandibular ramus of the Vth nerve appears on the floor of the orbit between the pterygoideus muscle on the inner side and the temporalis on the outer. It runs forward for a short distance along the medial border of the temporalis and then, above the antorbital transverse bar, it passes dorsally to the muscle, crossing it from within outward and forward. Under cover of the muscular process it perforates the depressor labii superioris longus. It next bends laterad and ventrad and crosses the outer and superior surfaces of Meckel's cartilage between the insertions of the temporalis and pterygoideus in front and the masseter and depressor mandibulae behind. Having crossed the cartilage of the lower jaw, it turns forward and was traced nearly to the symphysis ; the twig to the Csv.1b was clearly seen in several dissections. No twig was observed turning backwards to reach the interhyoideus muscle.

HYPOBRANCHIAL MUSCLES.

Two subarcuales recti are recognizable (Fig. 74, S.a.r.), but, as they extend further than across a single interbranchial interval and both arise from the first ceratobranchial cartilage, it were only guesswork to attempt their segmental designation.

They are two narrow, thin bands of fibres which run parallel, separated by a narrow interval. The medial muscle arises from the first ceratobranchial cartilage a little distance from the lateral edge of the planum hypobranchiale and passes back to be inserted into the third ceratobranchial* and hypobranchial plate just where the two are articulated. The lateral muscle arises laterally to the other and passes back and medially to be inserted into the point of articulation of the hypobranchial plate and the fourth ceratobranchial.

Only one subarcualis transversus (Fig. 74, S.a.t.) was found in tadpoles of this stage. It is a short thin muscle which arises from a spur on the centre-point of the second copula, first basibranchial cartilage, by a fine short tendon. It rapidly becomes wider as it passes laterad to be inserted into the bases of the first and second ceratobranchial cartilages just beyond the margin of the hypobranchial plate.

A single marginal muscle (interbranchial muscle) is indicated only at this stage by a fine brightly-stained line of tissue along the external surface of the first branchial cartilage. This is in the position in which the muscle itself is developed in stage B.

Innervation.—I have not been able to determine the innervation of these muscles.

The Claviculo-branchialis (Fig. 74, Co.br.).—This name is applied to a muscle very similar to the subarcualis transversus, which takes origin immediately behind it from the hypobranchial plate just at and medially to the root of the third branchial arch and, tapering, extends mediad, slightly caudad and ventrad to be inserted into the tissues of the pericardial wall.

Innervation not determined.

The Levator Hyoidei (Fig. 75, L.hy.) arises from the lateral edge of the meta-pterygoid process. This is an exceedingly fine triangular sheet of muscle fibres. The origin from the meta-pterygoid presents a short gap dividing the muscle into anterior and posterior halves, and suggestive of a duality of the muscle. The insertion is by the point of the triangle into the hyoid cartilage. The point of insertion is on the postero-lateral edge behind the insertion of the dilator hyoidei and posterior to that for the origin of the interhyoideus.

Innervation.—This is by twigs from the ramus hyoideus VII after it has been joined by the communicating branch from the IXth, and as the nerve passes under cover of the muscle.

The Dorsal Superficial Branchial Constrictors (Csd.3-6) are represented by an inconstantly interrupted sheet of fibres (Fig. 75, L.hr.) which arise from the lateral edge of the meta-pterygoid process behind the levator hyoidei and extend ventrad to be inserted into the outer wall of the branchial chamber along the mid-lateral line. The number of fasciculi into which the sheet is divided by the interruptions is three or four, and the situation of the fasciculi is not sufficiently constant to allow one to hazard an opinion as to actual number of superficial dorsal constrictors represented, basing that opinion on the structure of the muscle. On the other hand one is reasonably justified in postulating a number equal to that of the branchial arches.

---

* The four branchial arches are quite unsegmented so that the designation ceratobranchial or epibranchial is to be understood as purely topographical and one of convenience only. The distal or epibranchial ends of the arches are united by a serrated strip of cartilage which gives to them the appearance of having, each, bent posteriad till it came into contact and fused with that next behind.

Innervation.—It can be stated that these muscles are innervated by twigs from the ninth and tenth nerves, because these nerves only were found in their proximity. The extreme tenuity of the twigs, however, renders it extremely difficult to determine their origin, they are so easily torn loose in the attempt to dissect them out.

The Constrictor Pharyngei muscle arises from the postero-lateral and ventral corner of the auditory capsule. It passes caudad, mediad and ventrad around the posterior wall of the branchial cavity.* It does not reach the mid-line, but is inserted a little distance therefrom into the posterior and ventral wall of the branchial cavity.

The Cucullaris muscle arises medially to the constrictor pharyngei from the inner corner of the postero-ventral angle of the auditory capsule. From this origin it passes mediad and ventrad between the posterior branchial and anterior abdominal walls. At its origin and for a little distance therefrom it is narrow and ribbon-like and in this part of its length it is more closely related to the branchial wall ; at about the middle of the total length of the muscle it passes over the space between the two and becomes more intimately bound to the abdominal wall and, expanding fan-wise, it is inserted into a tendinous intersection, to the other side of which the anterior end of the rectus abdominis is attached. The line of this intersection is in the horizontal plane a little ventral to the middle of the dorso-ventral diameter.

Innervation.—The motor twig to the muscle was not found in any of the dissections of this stage, but, as it was subsequently demonstrated that this becomes the cucullaris muscle of the adult frog, one very naturally assumes that it is innervated, as is the adult muscle, by the Xth nerve.

The superficial ventral branchial constrictors.—Before describing the muscle which is believed to represent these muscles of the fish, it is necessary to recall the fact that the branchial arches bend ventrally as they extend laterally from their joint with the hypobranchial plate. The pericardium lies behind but in the plane of the triangular space thus formed below and between the branchial chambers. The whole of this space, which tapers to an apex immediately below and behind the second copula, is enclosed below by a relatively strong membrane which is attached on each side to the ventral convexity of the branchial arches, beyond this the arches are attached to the membrane as it rises on each side to gain an attachment to the lower margin of the meta-pterygoid process medial to the attachment of the levator hyoidei and superficial dorsal branchial constrictor muscles.

I return now to the ventral branchial constrictors (Csv.3). Traversing the floor of the pericardial space there are a series of transverse fasciculi which are inserted into a median raphe and which arise on each side along the lateral limit of the space. On each side posteriorly some of these fibres ascend further on the lateral wall of the branchial chamber to arise from a short longitudinal branchio-abdominal ligament which, later becoming attached to the coracoid, is recognizable in the adult frog as a coraco-cephalic ligament.

Innervation.—Though it cannot be definitely asserted, it is believed that this diaphanous muscle is innervated by twigs from the IXth and Xth nerves.

HYPOBRANCHIAL SPINAL MUSCLES.

The Geniohyoideus Muscle (Fig. 74, G.hy.) lies dorsally to the Csv.1a and 1b and to the interhyoideus. It is a narrow band of fibres which may be regarded as arising from the posterior margin of the hypobranchial plate. From this origin it passes directly forward, between the interhyoideus and the hyoid cartilage, and then dorsally to the two divisions of the first superficial ventral constrictor to be inserted into the inferior labial cartilage laterally to the tiny nodular primordium of the Csv.1a.

The Quadrato-abdominis Muscle is an exceedingly transitory structure. It was present in about 50% of the dissections of this stage, and provided evidence that they were not all in precisely the same stage of development. I have been unable to find the muscle in any of the earlier or later stages of this or other Anuran tadpole that I have been able to examine.

---

* When the skin has been removed from the venter of the tadpole it is found that one can quite readily separate the posterior branchial wall from the anterior abdominal wall on either side of and below the pericardium, and that this separation can be effected on each side right to the dorsal limit of the branchial cavity just below the cranial floor.

Lying superficial to all the other muscles, this takes its origin from a back-turned spur on the quadrate just behind the articular extremity. This spur projects ventrad, mediad and caudad, and carries the fine tendon of origin of the muscle quite clear of the depressor mandibulae, the cephalic head of which lies against its concavity. The tendon of origin begins as a fine thread and then becomes a ribbon which gives place to muscle fasciculi only after it has passed the posterior margin of the interhyoideus. The muscular part of the structure is extremely thin, little more than a single layer of fibres. These broaden out behind the interhyoideus and lose their identity on the surface of the anterior end of the rectus abdominis close on either side of the mid-line.

I am unable to homologize this muscle with any in the fishes. Innervation not determined.

Stage B. (Figs. 77, 78.)

Until the pectoral girdle is developed no changes in the musculature take place which call for description. The tadpoles of this (B) stage have, all of them, both limb-girdles developed. There is, however, so little change in size that the presence of the limbs alone serves to distinguish them from stage A before they are dissected. The mouth is as in stage A.

Intermediate stages display changes in the muscles which permit one to speak with confidence of the changes recorded in this. Those intermediate stages, it is believed, will be readily visualized by comparison of this with stage A.

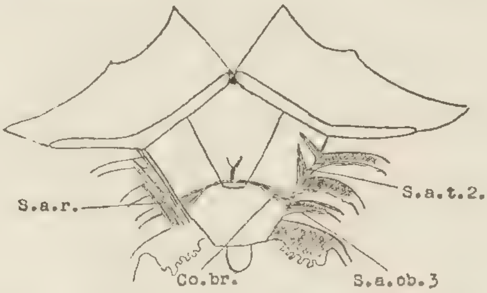


Fig. 77.—*Mixophyes* tadpole, stage B.—Ventral aspect.

The Csv.1a, though but very slightly increased in size, now shows quite clearly its muscular character.

The Csv.1b is somewhat broader antero-posteriorly but is not appreciably thicker.

The Interhyoideus also is changed only in that it is broader.

The Dilator hyoidei is unchanged, as also are the two heads of the depressor mandibulae.

The muscles of mastication present one particularly interesting change. The depressor labii superioris longus has become slightly shorter and it has acquired an insertion into the upper surface of Meckel's cartilage in front of that of the temporalis, as well as having still its original insertion into the superior labial cartilage. The temporalis muscle also is shortened slightly. The masseter is definitely enlarged. The remaining muscles of mastication are unchanged.

The subarcuales recti and transversi are unchanged.

The single interbranchial muscle is now definitely composed of muscle fibres, and the second and third interbranchials are recognizable at the same stage as this was observed in stage A.

The Coraco-branchialis now extends caudad to an insertion on the coracoid just medial to the glenoid cavity.

The Levator hyoidei is thicker than in stage A.

The Superficial Dorsal Branchial constrictors are also more definitely developed muscles, in that they are thicker and more compact.

The Constrictor Pharyngei is also thicker and now reaches nearer the mid-line.

There are now recognizable four muscles behind the branchial cavity. (These are semi-schematically represented in Fig. 78.)

The first of these is the Omo-hyoideus (Fig. 78, Omo.). It is a narrow ribbon of fibres which arise from the posterior wall of the cavity close to the ventral end of the fourth branchial cartilage and passes caudad to be inserted on to the scapula just laterally to the glenoid cavity.

The second is the Cucullaris (Fig. 78, Cu.). This is now much increased in thickness and is inserted on to the dorsal surface of the scapula laterally to the joint.

The third is the muscle which, in the adult, is the dorso-laryngeus. It arises under cover of the origin of the cucullaris and runs ventrad on the surface of the posterior branchial wall to terminate just laterally to the origin of the omo-hyoideus.

The fourth, and last, of these muscles (Fig. 78) arises from the ventral surface of the skull medially to the origins of the last two. It is a thin, relatively broad, band of muscle fibres which pass mediad and ventrad on the posterior branchial wall, near its dorsal limit, and ends thereon ventrally to the pericardium. The point of termination of this band of muscle fibres is near the middle of the curve of the fourth branchial cartilage but somewhat closer the mid-line. This band of fibres ultimately gives rise to the muscles which I have designated cranio-hyoideus and cranio-hyoideus anterior, two of the three posterior petro-hyoid muscles of Gaupp. These muscles are already indicated by incomplete divisions of the band of fibres.

The superficial ventral branchial constrictor sheet (Csv.3) is now more definite, it appears almost as a continuous sheet instead of as a wavy network of fibres as in stage A.

The Genio-hyoideus muscle has increased in width and almost reaches its fellow of the other side at the mid-line. It is also much shorter and terminates behind in a short tendon which is inserted into the hypobranchial copula.

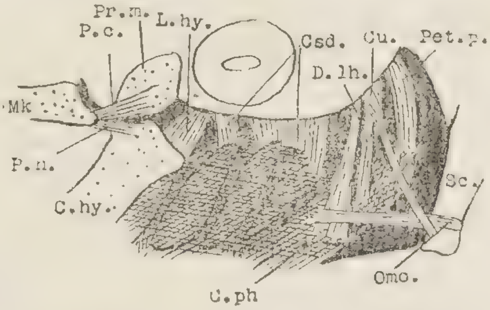


Fig. 78.—*Mixophyes* tadpole, stage B.—Lateral aspect.

The tiny genio-glossus, recognizable in earlier stages as a brightly stained tissue condensation, now appears as a definite muscle. It arises from the inferior labial cartilage superficially to the genio-hyoid on either side of the submentalis and terminates in an irregular brush of fibres amongst the tissues of the floor of the mouth, passing dorsad between the two genio-hyoid muscles to reach that tissue.

The Quadrato-abdominis muscle has disappeared.

The Infraspinatus and levator-scapulae muscles are recognizable. Though small, they are already quite as in the adult.

The final stages in the metamorphosis of these muscles into those of the adult frog have been studied in three later stages of *Mixophyes* and in a very complete set of stages in the development of *Limnodynastes*. It has been possible to compare stages in the development of the smaller *Limnodynastes* with stages A, B, C, D and E of the larger tadpole. This comparison revealed a very complete similarity and enabled one to use these stages as " mile posts " in the wider comparison.

The Csv.1a gives rise only to the small compact submentalis of the adult.

The Csv.1b extends first caudad on either side of the mid-line giving rise to the Csv.1b^1, then later, as the lower jaw lengthens backwards, a deeper layer of this muscle is carried back by the elongating lower jaw, and it is this which gives rise to the Csv.1b^2.

The Interhyoideus gives rise to the muscle which I have designated Csv.2, and which Gaupp terms the subhyoideus. No change is found in this muscle until the hyoid cartilage commences to assume definitely its elongated, curved and slender adult form. When this is first initiated the interhyoideus appears to become broader at the expense of its thickness, and its origin is carried dorsad, and caudad with the curving upper end of the stylohyal cartilage. This change commences after the tail has shrunken to about one-third of its full size. The final stages in the development of this muscle are those during which it increases in thickness and becomes folded on itself as described in the adult.

The Csv.3 appears to be entirely aborted. It is, however, possible that some of its anterior fibres are incorporated along the posterior margin of the Csv.2.

The Dilator Hyoidei is another caducous muscle. As the point of articulation of the lower jaw is carried posteriad the muscular antorbital process is gradually reduced in size, and just before the last stages in this transportation the hyoid cartilage loses its articulation with the inferior surface of the process and becomes attached loosely to the ventral surface of the auditory capsule. The dilator hyoidei becomes progressively reduced in keeping with the reduction of the muscular process, and finally disappears rapidly just prior to the alteration in the attachment of the stylohyal.

The Depressor mandibulae is developed directly from the two heads already present in stage A.

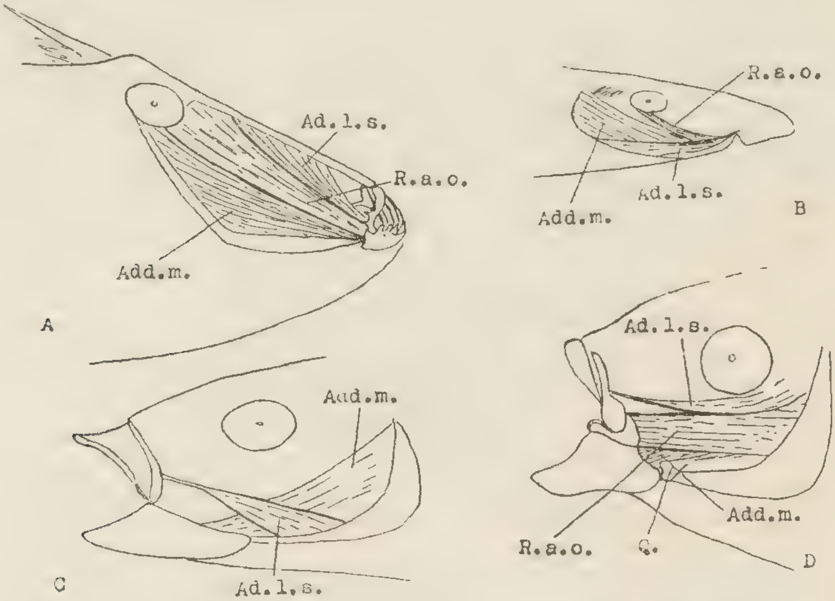


Fig. 79.—Four illustrations to show different origins of the same muscles in fishes.

The origin of the Pars Cephalognathica spreads so as to occupy the whole of the posterior edge of the muscular process under cover of the levator hyoidei. When the process has been transported caudad, this head of the muscle extends dorsad and caudad across the interval between the process and the auditory capsule to reach the site of origin it has in the adult.

The origin of the Pars Notognathica also is carried caudad as the hyoid articulation to the subocular arch is carried back. When the hyoid plate of the tadpole is transformed into the stylohyal cartilage of the adult this head of the muscle loses its origin from the cartilage and retains its superficial position, the origin being transferred to the subcutaneous deep fascia as in the adult.

The muscles of mastication change their direction as the jaw articulation is carried backward and slightly laterally.

The Depressor Labii Superioris Brevis has completely lost its identity in stage C of *Mixophyes* in which the mouth is just beginning to extend back and along the side of the skull, and whilst the superior labial cartilages still function as the upper jaw.

The Depressor Labii Superioris Longus retains its insertion into the upper labial cartilage until that disintegrates and is absorbed. This takes place very rapidly just after the tail has been completely absorbed and the tiny frog has left the water. During the change the animals are very lethargic and lie hidden beneath stones and other cover at the water's edge. For this reason I failed to observe the transition amongst the specimens of *Mixophyes* and was only successful with the *Limnodynastes* by fortunate chance. Several specimens at this stage of development were washed out whilst cleaning up the aquarium late in December, 1933.

After the upper labial cartilages are absorbed, the long depressor of the upper lip becomes partly incorporated with the Temporalis but, even in the adult, it is still readily separable as a superficial and lateral portion of that muscle.

The Pterygoideus and Temporalis alter only in their changed direction ; the former becomes the Pterygoideus of the adult. The Massetericus retains its primitive origin from the muscular process till that is aborted ; it then gains an origin from the inferior edge of the post-orbital bar and from the inferior and anterior margin of the tympanic annulus.

The Quadrato-mandibularis (Masseter) and Masseter minima first make their appearance whilst the last half of the tail is being absorbed, and they were found from the first in the situation they occupy in the adult frog.

The whole of the subarcual muscles are caducous, and they are aborted when the branchial skeleton is metamorphosed into the hyoid apparatus. A third subarcualis rectus and a second subarcualis transversus are developed at the time the fore limbs are formed but before they are protruded, and at this time the three interbranchial muscles are also fully developed.

The metamorphosis of the branchial skeleton is also accompanied by the complete abortion of the levator hyoidei, and the superficial dorsal branchial constrictors.

At this time also the Constrictor Pharyngei extends further mediad, meets its fellow of the other side behind the larynx and some of its fibres obtain a point of origin on the posterior horn of the hyoid skeleton.

The three petro-hyoid muscles also reach the adult condition as the branchial skeleton is metamorphosed, whilst the hyo-glossus appears and reaches the adult form and the genio-hyoideus becomes divided up into the component parts of the adult during the same period.

The laryngeal muscles of the late tadpole consist of a dorso-laryngeus and a Sphincter Laryngei, this latter being incomplete anteriorly and dorsally.

In addition to these the posterior fibres of the constrictor pharyngei are inserted into the same tissue as the anterior ends of the sphincter.

COMPARISON WITH *NEOCERATODUS* AND THE FISHES.

Watson (1926, pp. 194–5) wrote : " The extremely close resemblance between the Dipnoi and the Urodela, a resemblance covering the respiratory and circulatory systems, the urogenital apparatus, the brain, the skull, the histology and the embryology throughout, indicates them as the first fishes to be considered in the search for the Amphibian ancestors.

" These resemblances are specifically between the Dipnoi and the Urodela, they appear most strikingly in a comparison of Lepidosiren with a perennibranchiate Urodele, and are not nearly so pronounced if Ceratodus be compared with a frog or a Cœcillian."

This insistence on comparison with adult forms and the neglect of the larval stages of the remaining Urodeles and of the Anura is peculiar. Watson is probably correct in his statement on a later page of the same work that the aquatic amphibians are in all probability descended from terrestrial forms. But that he should overlook the fact that the aquatic forms may be regarded as having been arrested at one of the stages of development common to all Amphibia is regrettable. Had he not done so he would have found the Dipnoi to be comparable with all the recent Amphibia, with the possible exception of the aberrant Caecilians. Even in the latter, as we shall see later, the adult structures of the head indicate quite clearly that they too are comparable with those most primitive amphibians, the Dipnoi. Watson's description of *Neoceratodus* as a " modern fish " is quite incomprehensible.

The muscles of the anuran tadpole present a somewhat bewildering resemblance to the Dipnoi on the one hand and to the fishes on the other.

Let us consider first the muscles of the mandibular segment. The submentalis is unquestionably completely homologous with the similarly named muscle of the bony fishes. Behind this we find a very well defined intermandibularis equally unequivocably homologous with that of *Amia* or *Polypterus*. On the other hand, this last muscle is as clearly homologous with the intermandibularis of the Dipnoi. This is the more apparent when the tadpole muscle is compared with that of the 19 mm. larva of *Protopterus* (*vide* Edgeworth, 1926, plate IV, fig. 19). The Dipnoans, however, have no submentalis muscle.

Whilst the muscles of mastication may be broadly divided into two main groups, those arising medially to the rami mandibularis and maxillaris V, and those arising laterally thereto as in the Dipnoi, there has been a remarkable division of the latter group of muscles which can only be compared with that which has taken place amongst the fishes.

We may begin by recognizing as probably completely homologous the muscle having its origin medial to and in front of the nerve in all of these forms. It has been consistently designated the Pterygoideus in every description.

Several modifications of the M. levator labii superioris were observed amongst the Selachians. These are apparently illustrative of possible stages in the conversion of that muscle into the pterygoid adductor of the lower jaw. These were observed and described in various members of the Selachii and confirmed, it appeared, in the Holocephali and *Neoceratodus*. At the time of my study of the muscles of *Callorhynchus* (Kesteven, 1933) I was particularly struck with the fact that the masticatory muscles of the generality of the bony fishes might be divided into three components, which were then designated adductor labii superioris, retractor anguli oris and adductor mandibulae. The figures which were then published are reproduced again here (Fig. 79). They depict four stages in the change of the origin of the pterygoid muscle from anterior to the orbit to behind it. In all four instances the ramus mandibularis of the Vth nerve lies between the parts of the pterygoid muscle below and the temporo-masseteric muscle superficially.

In the tadpole the Pterygoideus muscle retains its primitive origin medial to the nerve and, as in the Dipnoi, it passes forward to its insertion on the lower jaw anterior to the point where the nerve crosses the jaw. Resembling in its origin also all those fishes which retain the primitive origin of the muscle.

The Temporalis is either the adductor labii superioris or the muscle which, in the work on *Callorhynchus*, I designated the retractor anguli oris. The insertion of this latter muscle is, in the great majority of the bony fishes, into the lower jaw and, per medium of a more or less definite tendinous condensation of the maxillo-mandibular fascia, into the maxillo-labial bone as well.

It now becomes clear that the origin of this muscle in the tadpole lateral to the nerve, and its dual insertion into both Meckel's cartilage and into the superior labial cartilage should be interpreted, in the light of our present knowledge, as indicating not only the complete homology of the muscle with part, at least, of the M. temporo-massetericus of the bony fishes, but also the complete homology of the superior labial cartilage of the cartilage of the tadpole and the maxillo-labial bone of the fishes.

These homologies are of particular interest as confirming the views already expressed that the labial bones of the fishes are not homologous with the maxillae and premaxillae of the tetrapods.

The homologies of the remainder of the muscles of mastication of the tadpole with those of the fishes are not subject to separate determination. The most that can be said at present is that they are, as a whole, to be regarded as derivatives of the M. adductor mandibulae.

The recurrence of the division of the adductor muscles of the jaw into two groups by the emergent rami of the Vth nerve, which was observed throughout the fishes, must surely be regarded as inherited by both fishes and amphibians from a common ancestor. If this be a reasonable assumption, it constitutes a complete justification for the opinion expressed in the last paragraph.

In the hyoid segment there are in the tadpole the interhyoideus, dilator hyoidei, the levator hyoidei and the depressor mandibulae, and, of these, the first and last give rise to adult muscles, the other two are entirely caducous.

Comparison with the larval *Protopterus* leads to the suggestion that the muscle which is here designated the levator hyoidei is that which Edgeworth terms the levator hyoidei, and if that be so, and if Edgeworth's identification be correct, then that which I have designated dilator is identifiable as the superficial dorsal hyoid constrictor. The interhyoideus is, apparently without doubt, homologous with the similarly named muscle in the *Protopterus* larva.

It is probable that the muscle which I have designated the Csv.3 is homologous with the constrictor hyoidei of Edgeworth's description. Edgeworth accepts the statement of Rudge that the muscle in question is innervated, in *Protopterus*, by the ramus hyomandibularis VII. Though unable to state so definitely, I am of the opinion that in the tadpole the Csv.3 is innervated by twigs from IX and X.

The superficial and deep ventral hyoid constrictors have been so exceedingly modified in the bony fishes that comparison of the tadpole muscles with them is difficult. This is the more so in view of the fact that the whole of the interhyoideus muscle becomes, in the tadpole, converted into a superficial constrictor in the adult, whilst in the bony fishes the primitive single muscle becomes developed into superficial and deep muscles. The very definite attachment of the muscle in the tadpole, to the lateral end of the hyal cartilage, would appear to be evidence that we have to deal with a true interhyoideus, as we know that muscle in the elasmobranch fishes, and that the posterior portion of the pars primitiva, which gives rise to the superficial muscle in the elasmobranchs, is not developed in the tadpole at all.

If it should subsequently be shown that the Csv.3 is really a caducous Csv.2, then it will also have been proven that the superficial ventral hyoid constrictor of the adult frog is developed from the interhyoideus, and is a deep constrictor which has acquired a superficial situation in replacement of the lost posterior portion of the pars primitiva ventralis hyoidea.

In the branchial segments we may first of all discuss and dismiss those muscles whose homologies are apparently quite clear. The musculi marginales are without reasonable doubt completely homologous with the interbranchial muscles of the Dipnoi and Elasmobranchs. The subarcualia obliqui and recti are also fairly certainly homologous with the similarly named muscles in the Dipnoi and bony fishes.

Although in the tadpole there is but one single slip representing the several present in both the Dipnoi and the Elasmobranchii, there is no reason to doubt that this single slip is homologous with one or other of the components of the coraco-branchialis.

The homology of the muscles which I have designated superficial dorsal branchial constrictors is by no means clear. In their situation on the wall of the branchial chamber, which is essentially an opercular fold, they would appear to be hyoid muscles and comparable with the dorsal end of the hyoid constrictor of the Holocephali and Dipnoi. On the other hand, they very definitely do not appear to be innervated by the VIIth nerve and they are quite definitely placed more deeply. They arise, not from a deep fascia, but from the edge of a cartilaginous shelf, the metapterygoid process, which stands out behind the quadrate, and above the branchial chamber. Now whilst this process is quite clearly not in any way homologous with that which overhangs the branchial chamber of the Dipnoi, one cannot entirely overlook, and disregard, the fact that it has come to occupy that situation. This gives rise to the suggestion that the muscles may be the levatores arcuum branchialium. It will be remembered that there is good reason to believe that the branchial levators are to be regarded as the deepest portion of the primitive constrictor sheet dorsally ; it is therefore not surprising that it should be difficult to decide, as the sheet is progressively reduced, just which part remains. It may, however, be observed that in the most primitive Elasmobranchs the branchial levators are found to continue the deep constrictors dorsad ; they are, as it were, the dorsal continuation of the interbranchial muscles. In the tadpole the musculi marginales, which we have seen to be homologous with the interbranchial muscles of the elasmobranch fishes, are placed more deeply than those which I have designated the superficial dorsal branchial constrictors.

In the Axolotl we shall find that the muscles which have been designated the branchial levators are definitely more superficially placed than the musculi marginales of the Axolotl. There appears every reason to believe that these muscles of the Axolotl are homologous with the muscles under discussion. In the Axolotl they arise from the fascia dorsalis, the deep fascia, and therefore arise in similar manner to the superficial constrictors of the elasmobranch fishes.

Although the evidence is not conclusive, it is believed that the designation which I have given these muscles is more correct than it would be to designate them branchial levators.

RANA.

After the work on the development and adult anatomy of the cephalic musculature of the Australian frogs had been completed I received ten stages in the later development and metamorphosis of *Rana pipens* from Professor H. W. Norris. I have again to express my gratitude to him for his continued assistance. My work on the Amphibia is based very largely on material he has presented to me.

The youngest of these is a tadpole, fully grown, with small hind legs and very small fore-limbs tucked deeply beneath the surface. The most advanced has but a mere stump of a tail, the mouth, relatively, is of adult size ; the last (almost amorphic) remnant of the gill filaments remains as a strand of tissue in front of the pectoral girdle on each side. In short, metamorphosis is almost complete. The other eight stages are intermediate between these, and each is slightly more advanced than the one before it. They are in fact a thoughtfully selected series of the most instructive stages in the late steps of the development of the cephalic and capiti-pectoral muscles.

Being of large size these specimens were all good dissection subjects, and they were excellently preserved. Before dissection they were carefully skinned and then stained with picric acid.*

These ten stages have been preserved, after dissection, in my collection and are marked *Rana pipens*, Nos. 1 to 10.

They are so essentially similar to comparable stages in the development of the Australian frogs that it were almost mere repetition to describe them. This essential similarity permits one to believe that the description which has been given on the previous pages of the development and metamorphosis of the cephalic and capiti-pectoral muscles may be accepted as being applicable to the Anura generally.

The metamorphosis of the mandibular muscles is very clearly presented in stages 4 to 10. It is noteworthy that all the divisions of the adductor muscles of the lower jaw found in *Mixophyes* and *Hyla* are to be found here with even greater ease than in those forms. The depressor labii superioris brevis is better developed. In stage 10 all the muscles elevating the lower jaw of the adult Australian frogs are quite well developed.

The ventral constrictors develop just as in *Mixophyes*.

The levator hyoidei is rather weaker in *Rana* than it is in *Mixophyes*; its evanescence is presented in the four stages 5 to 8.

The migration of the two heads of the depressor mandibulae is quite clearly shown in stages 6 to 10, and in stage 9 the last semi-transparent remnants of the dilator hyoidei are to be seen posterior to the tympanic annulus, superficial to the depressor. Earlier stages in its absorption are seen in stages 8 and 7.

The M. interhyoideus develops as in the Australian frog. Behind the interhyoideus, and separated from it by a marked interval, there is, in stages 1 to 5, the muscle which I have designated the inferior branchial superficial constrictor. In *Rana* this muscle arises from the dorsal fascia behind the skull at the mid-lateral line as a narrow ribbon. The fibres diverge slightly, so that, at their insertion into a raphe at the mid-ventral line, the muscle is broader than at its origin.

In no case can I detect any innervation by twigs wandering caudad from the interhyoideus. The muscle is entirely caducous; its reduction and final disappearance without ever making contact with the interhyoideus is quite strikingly presented in the stages 5, 6, 7 and 8.

The position of this muscle in this series appears to confirm my identification.

In *Rana* there is no question whatever that the muscles which I identified, in the Australian frogs, as the superficial branchial dorsal constrictors are completely caducous. They are rather more weakly developed than in *Mixophyes*, but are still at their full development at stage 5. Now at this stage the crowding together of the branchial arches, characteristic alike of the Holocephali, Teleostei and Amphibia, has placed the long axis of the gill slits right across the path these muscle fibres would have to take were they to grow down to reach the outer ends of the fibres of the constrictor pharyngei, and moreover the first gill slit extends well posteriorly to the posterior margin of the muscle fibres in question. From stage 5 to stage 10 one observes the gradual closure of the gill slits and the absorption of the gill filaments. They close from before backwards one after the other. The two edges are brought close together and partial closure results in a row of small perforations along the line of closure; later the perforations are closed. In stages 6 and 7 the gill clefts are almost completely closed and the gill filaments form a crowded spongy-looking mass between the posterior margin of the interhyoideus and the pectoral girdle. In stage 7 the superficial dorsal branchial constrictors have lost their staining properties to a slight extent, as all the muscles do as they commence to be absorbed. The strand of muscle fibres which is to give rise to the anterior petro-hyoid muscles is seen passing ventrad and mediad behind and deep to the degenerating gill filaments. In stage 8 the dorsal superficial constrictors have faded to a shadow and have acquired the semi-transparent appearance of late absorption stages. The anterior petro-hyoid muscles are differentiated from the common strand. The degenerating gill filaments form a narrower, more compacted, granular-looking mass.

---

* Experience has taught me that dissection specimens which have been stained in picric acid should be very thoroughly washed with several changes of spirit before being put away to keep. If this precaution is not taken they darken very much and the differential staining is almost entirely lost, all the tissues turning a dark bronze-green. I have also found that a better differential colouring is obtained by staining with carmine first and with picric acid afterwards, than is obtained with picrocarmine mixtures, but great care must be taken that the carmine stain is very light; for dissection purposes carmine very readily overstains in the absence of the picric acid.

The development of the Omohyoideus in *Rana* is as in *Mixophyes*, as also is the development of the Cucullaris.

3. The Urodele Larva. (Figs. 80–82.)

The following description and the illustrations are based upon a numerous collection of Axolotls for which my thanks are due to Professor H. W. Norris. Not only have I to thank him for the collection of Axolotls and adult *Amblystoma tigrinum*, but he has also given me sets of serial sections, cut in all three planes, of larvae from 6 mm. to 47 mm. in length.

The dissected specimens varied in length from 8 to 16·5 cm. and showed no noteworthy differences in their musculature.

In larvae six to ten millimetres long there is not sufficient differentiation of the mesoderm to permit of the identification of the muscle plates with any degree of confidence. In those measuring thirteen to fourteen millimetres in length, practically all the muscles of the largest larvae are recognizable. The differentiation of the mesoderm into the muscles apparently takes place very rapidly between the ten and thirteen millimetre lengths.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Submentalis, Csv.1a (Fig. 80), appears in the 13 mm. larva as a compact little bundle of transverse fibres placed immediately behind the anterior tips of Meckel's cartilages. This muscle alters with age only by increasing in size, at no time is there any median interruption of the continuity of the fibres from side to side. The origin is from the perichondrium of Meckel's cartilage in the larva and from the periosteum of the dentary in the older specimens.

The Intermandibularis, Csv.1b (Fig. 80), is also developed in the 13 mm. larva, and has the form it retains throughout life. On each side it arises from the cartilage, or bone, of the lower jaw for almost the whole length of the lower jaw, forming a complete intermandibular sheet. The fibres are inserted in the mid-line into a raphe.

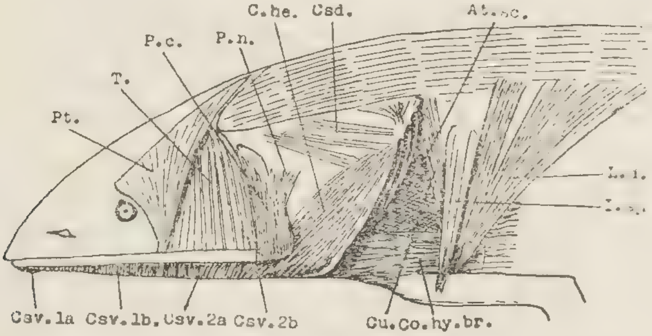


Fig. 80.—The Axolotl.—Lateral aspect of the subdermal muscles.

The adductor muscles of the lower jaw are not so much differentiated as in the anuran tadpole, only three being recognizable.

The Pterygoideus (Fig. 80, Pt.) is the muscle which previous writers have designated temporalis; Lightoller alone has recognized that it was not correctly so designated, and he recognized that it is really a pterygoid muscle.

The muscle has an extensive origin from the side and dorsum of the cranium in front of the quadrate, and above and medial to the auditory capsule so far back as the posterior dorsal ridge of the skull. In front the origin of the muscle extends forward of and above the orbit. From this extensive area the fibres converge to a tendon which is inserted on to the inner and upper edge of the mandible in front of the insertion of the temporalis.

The Temporalis Muscle (Fig. 80, T.) arises from the surface of the quadrate and auditory capsule between the depressor mandibulae and pterygoideus muscles. Its origin rises to a point at the level of the lateral intermuscular septum a little in front of the origin of the superficial dorsal constrictors and the apex of the area of origin of the depressor mandibulae. The fibres are gathered to an insertion on to the outer surface of the mandible close to its upper margin just a short distance in front of the joint. This insertion is effected by a very short tendon.

The Quadrato-mandibularis arises from the quadrate and auditory capsule under cover of the temporalis and laterally to the deeper portion of the pterygoideus. The insertion is into the inner surface of the upper edge of the mandible a short distance behind the insertion of the temporalis, with the ramus mandibularis V, penetrating between the dentary and Meckel's cartilage, placed between the two insertions. The fibres of the temporalis muscle have a general direction from above ventrad, cephalad and laterad, but they do not tend cephalad as acutely as the fibres of the underlying quadrato-mandibularis, which latter are thus recognizable from those of the more superficial muscle by the difference in direction, as well as by the fact that the ramus mandibularis V lies, in part of its course, in the cleavage plane between the two muscles.

The presence of this muscle has apparently not previously been discovered.

Innervation.—All three of the muscles of mastication are innervated by twigs from the ramus mandibularis V as it passes between them.

The Course of the Rami of Nerves V and VII.

The situation of the main divisions of the Vth and VIIth relative to the skull and the muscles is of interest and will be quite briefly reviewed.

The V-VII ganglionic mass is found partly embedded in the anterior wall of the auditory capsule close to the lateral wall of the neurocranium. From this ganglionic mass the two main divisions, V and VII, depart, the former antero-laterally, the latter postero-laterally.

The Nervus Trigeminus.—The first ramus to leave the trunk of the nerve is the ophthalmicus profundus. This runs forward along the inner wall of the orbit close to the floor. The maxillary ramus and ramus ophthalmicus superficialis next depart together. There is no reason to doubt that the ramus maxillaris is joined by the ramus buccalis VII in the Axolotl, as it is in *Siren*, and that a ramus ophthalmicus superficialis VII joins the ramus ophthalmicus superficialis V. Norris designates the combined trunks " infraorbitalis " and " supraorbitalis " in *Siren* (1913, p. 283).

The two nerves course alongside one another laterad and dorsad between the origin of the temporalis muscle and the anterior wall of the auditory capsule, posterior wall of the orbit, and come into view together beneath the skin high up behind the orbit. They turn forward at once over the surface of the pterygoideus muscle. The ophthalmicus superficialis courses directly forward above the orbit. The maxillary nerve turns ventrad across the muscle and then runs forward along the upper margin of the upper jaw below the orbit.

From the point of departure from the common nerve trunk of these last two rami the remainder of the Vth nerve, the ramus mandibularis, courses ventrad and slightly forward between the quadrato-mandibularis deep to it and the pterygoideus superficial to it, then between the quadrato-mandibularis and temporalis. Between the insertions of these two muscles it turns ventrad across the external, lateral, surface of Meckel's cartilage between it and the internal surface of the dentary bone. It thus reaches the ventrum of the mouth and breaks up into its terminal branches, which radiate mediad and forward from this point.

The Nervus Facialis.—The rami ophthalmicus superficialis and buccalis are, without reasonable doubt, incorporated with the last two rami of the Vth nerve.

The Ramus Palatini is given off close to the ganglion and courses straight forward beneath the cranial floor after a short course ventrad, mediad and forward.

I have not found the ramus alveolaris which Norris describes, but do not regard my failure as evidence of the absence of the nerve.

The main trunk gives off a relatively large communicating branch, the lateralis components, to the IX-X ganglion and then the large ramus hyoideus ; this, after a short course laterad and ventrad between the otic process of the quadrate and the cephalic head of the depressor mandibulae, turns backwards through that muscle and reaches the surface of the interhyoideus behind it and is distributed to structures on the ventrum of the mouth.

The two rami mentales are bound together for a short distance. After their separation they course together laterad and slightly dorsad between the quadrate and the cephalic head of the depressor mandibulae, and come into view beneath the skin fairly high up along the exposed margin of the quadrate. The ramus mentalis internus now runs down and forward along the exposed edge of the quadrate and then turns forward along the lower jaw. The ramus mentalis externus curves backward around the margin of the depressor mandibulae and then runs ventrad and slightly caudad on the surface of that muscle near its anterior margin. Finally it turns forward behind the insertion of the muscle and crosses the muscle in a cephalo-dorsad direction. It crosses superficially to the ramus mentalis internus behind the angle of the mouth and runs forward in the upper lip to just in front of the orbit where it receives a communicating branch from the ramus maxillaris V-VII. I have failed to find that branch of this nerve which, in *Siren*, runs along the ventral border of the lower jaw, or, it may be, I have failed to find the ramus mentalis internus, but if the latter, then the division of the ramus mentalis into two branches certainly takes place as just described. I have traced these nerves in several specimens.

THE MUSCLES OF THE HYOID SEGMENT.

In the 9–10 mm. larva the hyoid mesoderm forms a complete plate in which the differentiation into muscle plate and procartilage is not obvious, and in this respect it resembles the mesoderm of the remaining cephalic segments. It is, however, believed that certain more closely gathered strands of cells, which are slightly more granular and placed nearer the mid-line on each side, are to be regarded as the ectoderm from which the cartilage will later develop. There is certainly no division of the primordial muscle plate into its later components. In the 13 mm. larva (Fig. 81) the hyoid musculature consists of (1) a thin sheet of transverse fibres which extends from the posterior margin of the Csv.1b to the posterior edge of the opercular fold and extends upward on each side to the dorsal limit of the fold, arising from the deep subcutaneous tissues in this situation, and inserted into a median raphe ventrally, (2) a compact bundle of fibres which arise from the tissues dorsally to the end of the dorsal end of the hyoid cartilage and extend forward and ventrally beneath that cartilage to be inserted into its anterior tip, and (3) the depressor mandibulae.

The Csv.2 (interhyoideus of Drüner) is the continuous sheet, whilst the compact diagonal muscle is the Interhyoideus (cerato-hyoideus externus of Drüner).

In the larger Axolotls one can distinguish two portions of the Csv.2.

The Csv.2a (Fig. 80).—The anterior and major portion of the ventral superficial hyoid constrictor is very similar to the Csv.1b. It arises from near the dorsal end of the cerato-hyoid cartilage behind the jaw, and its fibres pass ventrally and forward, from above and posterior to the mandible, and then mediad and forward to be inserted into the median raphe. The great obliquity of the more anterior fibres carries them forward deep to the posterior half of the Csv.1b at their insertion. As these fibres come forward and ventrally from above and behind the posterior end of the jaw they have a very deceptive appearance of arising from the inner surface of the jaw itself.

The Csv.2b (Fig. 80).—This posterior portion of the hyoid constrictor arises from the superficial surface of the interhyoideus muscle behind the mandible and also from the dorsal tip of the first epibranchial cartilage. In the older larvae the two muscles are fused, but in the smaller it is possible to dissect the Csv.2b free from the interhyoideus right up to the tip of the epibranchial cartilage. The fibres of Csv.2b are parallel with those of Csv.2a and are inserted behind them into the median raphe. The most posterior fibres lie in the free edge of the opercular fold.

The Depressor Mandibulae in the 13 mm. larva presents (Fig. 81) a pars cephalognathica (Pc.) which is a compact bundle of fibres that pass almost directly dorsad to their origin from the connective tissues above the postero-lateral corner of the auditory capsule, and a very short and much smaller little bundle of fibres, the pars notognathica (P.n.), which arise from the ceratohyal cartilage just behind and a little above the posterior end of Meckel's cartilage. Both parts are inserted into the posterior end of Meckel's cartilage.

In the larger larvae the muscle presents only a pars cephalognathica. This arises from the dorsum of the skull behind the auditory capsule and in line with the intermuscular septum between the dorsal and lateral trunk muscles. Some of the posterior fasciculi arise from the connective tissue of the gill cover ventrally to the superficial dorsal branchial constrictors, and in front of the origin of the posterior fibres of Csv.2b. This, however, is only found in the largest specimens. The insertion of the muscle is on to the outer surface and posterior end of the mandible behind the joint. In the largest specimens (Fig. 80) the insertion is by a short stout tendon on to the extreme posterior end of the mandible.

The Interhyoideus (Figs. 80–82).—This is the muscle which has been designated cerato-hyoideus externus by Drüner (1903) and other observers. The muscle arises from the deep fascia close to the dorsal end of the first epibranchial cartilage just posterior to the top of the first gill cleft. It passes ventrad and cephalad in the opercular membrane, along the ventrum of the ceratohyal, to be inserted into that face of the cartilage from the angle thereof to the anterior tip. The two muscles do not meet in the mid-line.

Innervation.—The muscle is innervated by twigs from the ramus jugularis of the hyoid trunk of the VIIth nerve.

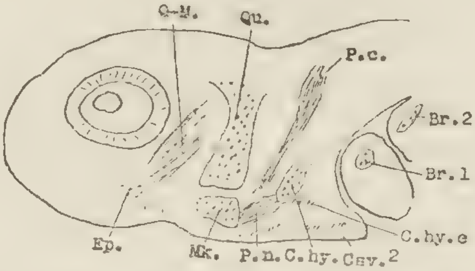


Fig. 81.—The Axolotl.—Sagittal section from a 13 mm. embryo.

MUSCLES OF THE BRANCHIAL SEGMENTS.

The Superficial Dorsal Branchial Constrictor muscles (Fig. 80, Csd.) number four. They are narrow bands of fibres which arise close together from the lateral intermuscular septum and fascia dorsalis behind the depressor mandibulae. From their origin they pass with varying degrees of obliquity to be inserted into the free edge of the opercular membrane between the branchial septa. The first of these passes deep to the dorsal end of the Csv.2b to reach the base of the first external branchia, the second and third reach the bases of the second and third external branchiae without passing beneath any other muscle, the fourth, Csd.6, ends in the free edge of the membrane ; there is no fourth external branchia.

Innervation.—Twigs of the IXth and Xth nerves were traced to these muscles in the larger larvae.

The Interbranchial Muscles (Musculi marginales) (Fig. 82, Mm.1–3) or first, second and third branchial muscles of Drüner, arise from connective tissues close to the tips of the second, third and fourth epibranchial cartilages and pass thence, parallel to the interhyoideus, to be inserted, the first into the base of the first epibranchial cartilage, the second and third along the length of the respective interbranchial septum, between the second and third epibranchial cartilages and the free edge of the septum. The second is shorter and more slender than the first, and the third than the second. Each of these muscles, at its insertion, is apparently in continuity with one of the dorsal superficial constrictors, but closer examination discloses that whereas the constrictor is placed quite superficially across the roof of the branchial chamber, these are placed on the deep side of the opercular membrane and pass more deeply as they extend ventrad and mediad.

Innervation.—These muscles are innervated also by twigs of the IXth and Xth nerves.

The Constrictor Pharyngei (M. transversus ventralis of Lightoller) (Fig. 82, C.ph.) appears in the larger larvae as a single muscle, but in the smaller larvae, from 40 mm. to 13 mm., there is a definite division of the muscle into anterior and posterior positions. According to Drüner the muscle represents fourth and fifth interbranchial muscles.

In the larger larvae it arises on each side from a little more than the middle third of the length of the fourth epibranchial cartilage and passes mediad to meet its fellow of the other side. The insertion along the mid-line is into the posterior one-half of the elongated basibranchial cartilage and into a median tendinous strand for a similar distance behind it. The muscle is a good deal broader antero-posteriorly at its insertion than it is at its origin.

Innervation.—It has not been possible to find the motor nerves to this muscle in any of the dissections. On the other hand, in a very fine series of horizontal sections of a 30 mm. larva stained with iron haematoxylin, it has been possible to trace the nervus intestino-accessorius and to observe its division, and finally to follow the ramus intestinalis recurrens sufficiently far to feel confident that the innervation of the muscles by this nerve in the Axolotl is probably as described by Norris (1913) in *Siren lacertina.*

The Dorso-laryngeus Muscle arises from the lateral intermuscular septum and fascia dorsalis immediately behind the fourth dorsal superficial constrictor and superficially to the antero-dorsal corner of the origin of the cucullaris. It passes ventrad and comes to lie parallel with, but deep (dorsal) to the posterior margin of the constrictor pharyngei and follows these around to be inserted into the median raphe on the floor of the pharynx just in front of the larynx. The fibres of this muscle are absolutely continuous from origin to insertion. Stained and cleared preparations show no sign of any interruption across the muscle.

Innervation.—This is probably by twigs from the nervus intestino-accessorius as in *Siren.*

Hypobranchial Muscles.

All these muscles are innervated by the ramus intestinalis recurrens. Norris (*l.c.*, p. 233) points out that there is here an invasion and capture of the territory of the primitive post-trematic rami of the branchial nerves by this nerve, which, he says, is accordingly much enlarged.

The Subarcualis obliquus 1 (Fig. 82, S.a.r.^{1}).—This is the muscle which, following Drüner, writers have designated the cerato-hyoideus internus. I have made use of the above designation in order to preserve in the nomenclature its homology with the muscle in the fishes and Dipnoi.

It arises from the ceratohyal close to the insertion of the interhyoideus, and passes backwards and slightly laterad to be inserted on to the ventral surface of the enlarged base of the first epibranchial cartilage.

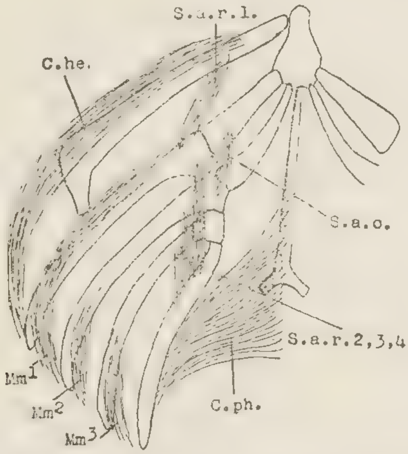


Fig. 82.—The Axolotl.—Ventral aspect of the branchial skeleton and its muscles.

Innervation.—This is by a twig which leaves the post-trematic branch of the glossopharyngeal nerve just before it passes beneath the muscle. Norris states that in *Siren* there is also a motor supply to this muscle from the ramus intestinalis recurrens. I have not found this second motor nerve, but would not imply that it does not exist.

The Subarcualis Obliquus 2 (Fig. 82, S.a.o.) arises from the outer end of the first ceratobranchial cartilage and is inserted in two separate bundles of fibres into the proximal end of the second epibranchial cartilage. This is the subarcualis obliquus of Drüner and others.

Innervation by the Xth nerve is as described by Norris.

The Subarcualis Rectus of Drüner (Fig. 82, S.a.r.) is clearly composed of three small muscles which are confluent along their contiguous margins. They arise from the bases of the first, second and third epibranchial cartilages and are inserted alongside of one another into the base of the fourth epibranchial.

Innervation is the same as that of the last muscle.

The Hypobranchial Spinal Muscles.

The Genio-hyoideus is a narrow muscle which arises from the mandible just laterally to the submentalis and passes directly caudad, beneath the superficial ventral constrictors, to be inserted on to the anterior edge of the short cornu of the elongated rod-like basibranchial cartilage, and to be then continued caudad by a similar but much shorter section which arises from the posterior edge of the same cornu and is inserted into the first tendinous inscription of the rectus abdominis.

The Claviculo-hyoideus (Fig. 80, Co-hy-br.) muscle has been designated by previous writers the omo-arcualis and the procoraco-arcualis ; I have preserved in my designation its homology with the muscle in the Dipnoi and bony fishes.

The muscle arises from the inferior surface of the basihyal, the inner ends of the first and second ceratobranchial cartilages, from the side of the elongated, rod-like basibranchial and both surfaces of the small cornua of that cartilage. The muscle walls-in the pericardium below and on both sides, it increases rapidly in bulk posteriorly, is interrupted twice by tendinous intersections just in front of the shoulder-girdle, and finally merges completely with the metamerically interrupted abdominal muscles, under cover of the shoulder-girdle.

The Genio-glossus muscle arises on each side from the mandible deep to the submentalis just to one side of the symphysis. It is composed of a narrow ribbon of fibres which pass directly caudad to be inserted on to the anterior edge of the posterior cornu of the basibranchial cartilage. These two cornua are so completely clothed by the coraco-branchialis that the genio-hyoideus appears to be inserted on to the ventral surface of this other muscle.

The Capiti-pectoral Muscles.

The Infraspinatus and Latissimus Dorsi muscles are included here in order to establish the position and relations of the Cucullaris and Attrahens Scapulae muscles.

The Cucullaris (Fig. 80, Cu.) arises from the lateral intermuscular septum and fascia dorsalis at the level of the septum immediately behind the last superficial dorsal constrictor, its anterior fasciculi being deep to the dorso-laryngeus muscle. The muscle is not very broad at its origin and the fibres converge to a fine tendon which is inserted into the scapula just above the glenoid cavity. This insertion is covered by the lower end of the infraspinatus.

The Attrahens Scapulae (Fig. 80, At.Sc.) arises by a fine tendon from the postero-ventral edge of the cranium just laterally to the origin of the lateral trunk muscles. The muscle expands into a thin narrow ribbon as it extends directly backwards, with a slight inclination ventrad, beneath the cucullaris and dorso-laryngeus to be inserted into the anterior margin of the suprascapula. At its insertion it is covered by the cucullaris.

The Infraspinatus (Fig. 80, S.sp.) arises from the suprascapula along its dorsal edge and passes down to be inserted into the outer side of the humerus near the head of the bone.

The Latissimus Dorsi (Fig. 80, L.D.) arises from the fascia dorsalis at the level of the lateral septum ventrally to the fifth, sixth, and seventh dorsal myomeres. From this relatively broad origin the fasciculi converge to a thin broad tendon which is inserted on to the inner side of the humerus opposite the infraspinatus.

COMPARISON WITH THE ANURAN TADPOLE.

The muscles of the mandibular segment.—The ventral superficial constrictors differ only in that the Csv.1b is more extensive in the urodele than in the anuran larva.

In the identification of the pterygoideus I have been guided by the relation of the muscle to the ramus mandibularis V. The muscle resembles that of the anuran tadpole in this relation, but differs in that it is inserted in front of the temporalis. This is a return to the more primitive situation of the two insertions relative to one another which was observed in the elasmobranch and many of the bony fishes.

It seems probable that we should be correct to regard the temporalis muscle of the urodele larva as containing in its posterior portion the fibres which form the masseter of the later anuran tadpoles. At no stage in the development of these muscles was a definite retractor anguli oris or depressor labii superioris observed in the urodele larva, though in sections of the 13 mm. larvae an antero-dorsal group of fibres of the temporalis have the appearance of being inserted into the tissues of the lip at the side of the mouth, but it is possible that this is only due to the forward bulging of the belly of the muscle above and in front of its insertion. On the whole it appears wiser to assume that the anterior portion of the temporalis which functions for a while as the depressor of the upper lip in the anuran larva is never so developed in the urodele.

The quadrato-mandibularis of the urodele must be accepted as representing the massetericus as well as the quadrato-mandibularis of the tadpole.

The superficial ventral constrictors in the hyoid segment present a partial return to the condition of these muscles in the fishes.

A typical Csv.2 is developed as in the elasmobranch fishes and Dipnoi. This forms a continuous sheet beneath the branchial arches just as in the Dipnoi, but is not interrupted by any skeletal structures on either side as it rises to its origin from the fascia dorsalis. In the older Axolotls the extent of its origin is reduced by the relative backward growth of the lower jaw.

Deep to this Csv.2, there is developed the muscle which has been designated the ceratohyoideus externus. Although the muscle fails to reach its fellow in a mid-ventral raphe, its development from the deeper and anterior portion of the hyoid muscle plate leaves no choice in the matter ; we are practically compelled to recognize this as homologous with the interhyoideus of the elasmobranchs and with part, at least, of the protractor hyoidei of the bony fishes.

4. Perennibranchiate Urodele.

NECTURUS (Figs. 83–84).

The following description is based on the dissections of *Necturus maculatus*. This dissection has been carried out with Wilder's account of the muscles of the head of *Siren lacertina* (1891) and Norris's account of the Cranial Nerves of the same species (1913) open beside me. It will be found that, in the main, the muscles of *Necturus* are similar to those of *Siren*, and the Axolotl.

MUSCLES OF THE MAXILLO-MANDIBULAR SEGMENT.

The Submentalis is, relatively, a smaller muscle than in the Axolotl.

The Intermandibularis is essentially the same.

Wilder has confused the posterior portion of this with anterior part of the Csv.2a. He describes an intermaxillaris anterior which includes the Csv.1a, Csv.1b and the Csv.2a. The gap which he describes between the fibres of his intermandibularis anterior laterally is quite obvious in both the Axolotl and *Necturus*, but it lies between the posterior margin of the Csv.1b and the anterior margin of Csv.2a.

The muscles of mastication are remarkably massive.

The Temporalis (Figs. 83–84) (Masseter of Wilder, and of Norris, who in the main adopts Wilder's nomenclature).—The three portions which Wilder describes are not recognizable in *Necturus*, nor is it possible to recognize any boundaries whereby one may determine the portion of this muscle which should be regarded as homologous with the quadrato-mandibularis of the Axolotl. The origin of the muscle is extensive ; it is from the whole of the lateral surface of the skull behind the foramen for the V-VII nerve trunks. This area comprises the anterior surface of the quadrate, where that lies upon the otocrane, the anterior otocranial wall medial to the quadrate, and the lateral one-half of the dorsum of the skull. Medial to the muscle lies the pterygoideus muscle, and between them a strong fascial partition which Wilder designated the ligamentum intermusculare anterius. The median fibres of the temporalis muscle arise from the outer surface of this fascia almost as far forward as the posterior boundary of the orbit. The fibres arising from the fascia form a small antero-median portion of the muscle which is separated from the rest by a cleavage plane which, however, does not extend the full depth of the muscle. The posterior, and main, mass of the muscle bulges backward and ventrally beyond the posterior limit of its insertion and this portion covers, almost completely, but is in no way attached to,

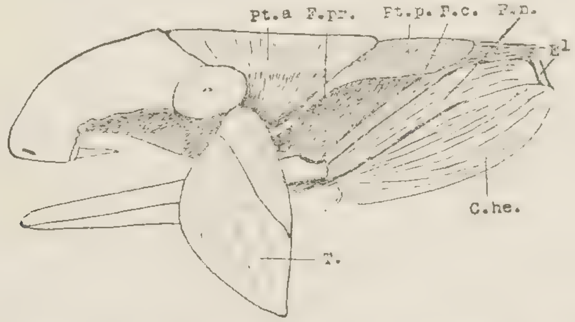


Fig. 83.—*Necturus.*—Lateral aspect of the more superficial muscles. The M. temporalis has been detached from its origin and turned down.

the depressor mandibulae. Deep within this part of the muscle there is a tendon, as described by Wilder, into which the fibres are inserted. The fibres of the antero-median portion of the muscle are attached to the median border of this central tendon towards its deep margin. The tendon emerges from the anterior edge of the muscle immediately below the orbit and is inserted into the tip of the low coronoid process of the mandible and then runs along the upper and outer edge of the mandible, becoming blended with the deep fascia of the lower lip and perichondrium of the jaw.

It is not found possible to define any clean or nearly clean cleavage plane in this muscle, which would indicate the possible boundary between components comparable with the temporalis and quadrato-mandibularis of the Axolotl.

Innervation.—The motor supply to this muscle leaves the main trunk of the Vth nerve actually before the various rami have separated. Doubtless, microscopic examination would reveal that it is a branch of the R. mandibularis.

The Pterygoideus.—This muscle was described by Wilder as the temporalis. As in *Siren*, two parts of the muscle can be recognized dorsally.

The Pars Posterior (Fig. 83, Pt.p.) is the smaller part. It arises from the dorsal median intermuscular septum (ligamentum intermusculare mediale, of Wilder), the fascia covering the anterior end of the dorsal trunk muscles and a small area of the dorsum of the skull just in front of the origin of these last muscles. The muscle has a central tendon into which the fibres are inserted. Those arising from the intermuscular septum are inserted into the median surface of the tendon, those from the other origins into its outer surface. The muscle tapers as it passes rostrad, laterad and ventrad ; from its anterior apex the tendon issues and continues in the same direction to become attached to the inner surface of the tendon of the temporalis muscle in front of all its fibres and just above and behind the insertion into the conoroid process of the jaw.

Innervation.—Just where the tendon issues from amongst the muscle fibres this muscle passes directly dorsad of the foramen prooticum from which the Vth and VIIth nerves issue. The motor twig to the muscle rises directly from the crowded branches of these nerves as they issue from the foramen. Doubtless it comes from the R. mandibularis V, but this could not be demonstrated by dissection.

Pars Anterior (Fig. 83, Pt.a.).—This is very much the larger part of the muscle and has an extensive origin. It arises from the dorsum of the skull from medial to the auditory capsule posteriorly, forward, till its anterior margin lies above and medial to the anterior boundary of the orbit ; also from the sloping lateral surface of the anterior process of the parietal bone, which extends forward laterally to the frontal to reach the low antorbital prominence. This latter, however, really lies a little posterior to the anterior boundary of the eye. A third area of origin is situated below the second and extends neither so far forward nor so far back. This area is the sulcus in front of the ophthalmicus profundus and optic foramina and the upper surface of the os transversum lateral to the sulcus.

The whole of the fibres are gathered to a short, relatively broad, tendon which is bound to the inner surface of the mandible for a short distance in front of the joint. The anterior fibres and anterior margin of the tendon pass below the eye to this insertion.

Innervation.—This also is by a nerve which was traced only to the closely packed branches of the V-VII complex in the opening of the foramen prooticum, again doubtless a branch of the R. mandibularis V.

The deep portion of this muscle, that arising from the sulcus in front of the ophthalmicus profundus foramen, is very certainly the muscle which Norris illustrates and identifies as the pterygoideus (Norris, *l.c.*, Figs. 10 and 11). Although it is separated from the rest of the muscle by a slight gap at its origin, along which the deep ophthalmic and optic nerves run, it is not possible to separate the fasciculi from those of the rest of the muscle without dividing the fasciculi. It is not possible to regard this portion as a separate muscle, but it is of particular interest as foreshadowing the division of the pterygoid into the partes internus and externus which will be found in the reptiles. It is probable that this is the muscle which Wilder describes as the pterygo-maxillaris, although it is markedly different from the muscle in *Siren* as he describes it. It is very definitely not wrapped around the inferior surface of the mandible at its insertion to become subdermal as he describes. Norris depicts the ventral end of the muscle in *Siren* and shows it subdermal (Norris, l.c., Fig. 11).

The ramus mandibularis V, when it leaves the foramen prooticum, turns sharply laterad and slightly dorsad and then turns ventrad through the temporalis muscle, a good deal closer to the deep surface than to the superficial. It reaches the upper edge of the ramus of the lower jaw behind the insertion of the temporalis and then turns forward along the jaw. It follows from this that the whole of the pterygoid muscle lies medial to the nerve. The composite supraorbitalis and infraorbitalis trunks also issue from the foramen prooticum, they run directly forward with but a very slight inclination dorsad on the lateral surface of the pterygoid muscle medial to the ligamentum intermusculare anterior, the one turning laterally at the posterior boundary of the orbit, the other medially and dorsally, to pass one below and the other above the orbit.

MUSCLES OF THE HYOID SEGMENT.

The ventral constrictor sheet is essentially similar to that of the larger Axolotl. It will be remembered that in the smaller of those the Csv.2b could be traced dorsally to the upper end of the cerato-hyoideus externus, but that in the larger specimens this was not possible. In *Necturus* the origin of the Csv.2b is from the fascia covering the cerato-hyoideus externus, interhyoideus, along a line which runs horizontally caudad from the posterior end of the lower jaw to the root of the first external branchia, that is to say, which crosses the interhyoideus just where it turns dorsad behind the angle of the jaw. Wilder (1891) designates the Csv.2 " intermandibularis posterior ". Drüner (1903) terms the Csv.2a the " interhyoideus ", and the Csv.2b he calls the " cephalo-dorso-pectoralis " or sphincter colli.

Innervation.—Norris says that the branch of the R. mandibularis V which pierces the ramus of the jaw divides into anterior and posterior divisions after its emergence on the inferior and internal surface thereof. He further says that the posterior division innervates the posterior portion of the intermandibularis posterior and the anterior portion of the interhyoideus. That the interhyoideus should be innervated by a branch of the Vth nerve was quite unexpected and a very careful search was made for this posteriorly trending division. It was found, on both sides of my specimen, that the nerve divided, very soon after its emergence from the mandible, into anterior and posterior divisions, but the posterior division passed almost directly mediad, with but a slight trend caudad, and on both sides it was found to terminate before the very definite break between the anterior margin of the Csv.2 and posterior margin of Csv.1 was reached.

The ramus jugularis of the VIIth nerve was traced, just as Norris describes, on to the Csv.2 below the interhyoideus, cerato-hyoideus externus, and was found to send branches back to its posterior margin as well as forward nearly to the anterior margin.

The Depressor mandibulae (Digastricus, Wilder ; Cephalo-dorso-mandibularis, Drüner).—This muscle is more compact than is that of the Axolotl, the two parts are well defined.

Pars Cephalognathica (Fig. 83, P.c.).—This arises from the back of the suspensorium and the otocrane ; it is a narrow muscle deeper than it is broad. Insertion is by a short tendon, common to both parts of the muscle, into the posterior end of the mandible. The upper half of the deeper surface of this muscle is closely knit to the levator hyoidei. Wilder apparently failed to recognize this fact and describes the two together as the anterior portion of the digastricus.

Pars Notognathica (Fig. 83, P.n.).—The origin of this more massive part of the muscle is from the top of the first epibranchial cartilage and from a strong branchio-cephalic membrane which forms the roof of the anterior part of the branchial chamber. This membrane is attached in front to the postero-inferior edge of the suspensorium and otocrane medial to it and, extending horizontally backward, is bound to the upper half of the first epibranchial cartilage. The inferior surface of the skull immediately in front of its line of attachment forms the roof of the mouth, and this membrane carries the mucosa of that roof to the first branchial arch. The fibres of the muscle pass rostrad and ventrad to their insertion.

Innervation.—The pars cephalognathica is innervated by a branch from the hyomandibular trunk of the VIIth which divides to supply this muscle and the levator hyoidei. The nerve to the pars notognathica comes from the ramus jugularis. I only find one such ; Norris describes two in *Siren*.

The Levator Hyoidei (Fig. 83, L.hy.) is a small compact muscle which arises from the back of the otocrane and the branchiocephalic membrane deep to the upper end of the pars cephalognathica of the last muscle. The fibres are inserted into a thin tendon which is continued ventrad to be inserted on to the back of the ceratohyal just below the tip.

Innervation.—This is, as already described, by the same branch of the truncus hyomandibularis VII as innervates the muscle which covers it.

This muscle is of some interest on account of its presenting a partial fusion of the levator hyoidei and the pars cephalognathica of the depressor mandibulae. Although intimately knit to the more superficial muscle it may be separated, leaving clean cleavage surfaces. The tendon, however, is more closely bound to the deep margin of that of the depressor, though here also there was found a very definite narrow band of lighter texture between the two, indicating quite clearly the line of union.

Edgeworth describes and illustrates this muscle in 14½ mm. embryos of *Necturus*. He believed it to be a transient stage in the development of the depressor mandibulae (1911, p. 215). It is also present in *Siren* (Drüner and Norris).

The Interhyoideus (Fig. 83, C-H.e.) (Cerato-hyoideus externus, Wilder, Norris and Drüner).—This arises from the ventral surface of the ceratohyal, the area of origin extending from close to the inner, and anterior, end of the cartilage back to behind the posterior end of the mandible. The insertion is on to the spur of the first epibranchial cartilage just lateral to and below the origin of the pars notognathica of the depressor mandibulae and from the branchio-cephalic membrane just in front of the cartilage. The muscle is remarkably massive and bulges backward beyond its surface of origin. The deep surface of the muscle is clothed by a membranous tendon into which the fibres arising from the ceratohyal are inserted and which is itself inserted into the branchio-cephalic membrane. The fibres inserted into the epibranchial cartilage arise from a dense superficial aponeurosis.

Innervation.—By a branch from the ramus jugularis VII after that for the pars notognathica of the depressor mandibulae has been given off.

The cerato-hyoideus internus (cerato-branchialis) is not one of the hyoid muscles, it is described below as the subarcualis rectus I.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

These have been described by Drüner and by Wilder ; the synonymy is as follows :

This work.	Drüner.	Wilder.
Subarcualis rectus (I)	Ceratohyoideus internus	Ceratohyoideus internus
Subarcualia recti II-IV	Subarcualia recti	Constrictor arcuum branchialium
Superficial dorsal branchial constrictors	Levatores arcuum branchialium	Levatores arcuum
Subarcualia obliqui	Subarcualia obliqui	Protractor arcus ultimi
Interbranchiales.	Branchiales.	Depressores Branchialium.
Mm. marginales	Interbranchialis III	Hyo-trachealis
Constrictor pharyngei	Interbranchialis IV	Dorso-trachealis
Dorso-laryngeus	Dorso-laryngeus A and B	Dorso-laryngeus

The Subarcualis Rectus I (cerato-branchialis) arises from the posterior surface of the median end of the ceratohyal and from the basihyal alongside of it. The muscle is a small flattened spindle of fibres which pass almost directly caudad with a slight inclination laterad to be inserted into the distal end of the first ceratobranchial and median end of the first epibranchial.

Innervation (After Norris).—By a combined nerve formed by anastomosis of terminal motor twigs of the post-trematic rami of IX and of the second branchial nerve, this latter being a branch of the Xth.

The Superficial Dorsal Branchial Constrictor muscles are four in number; they arise from the fascia dorsalis along a curved line which commences in front at the postero-dorsal corner of the superficial surface of the pars cephalognathica and extends caudad with a convexity dorsad to the antero-dorsal corner of the suprascapula and infraspinatus muscle. The fibres of the first muscle pass nearly horizontally caudad to be inserted on to the tip of the first epibranchial above the origin of the pars notognathica.

Innervation.—This is apparently the muscle, of which Norris describes the innervation, under the designation second branchial levator. He describes the first levator as being innervated by the first branchial nerve, ramus post-trematicus IX. This holds true for the deep levator of the first arch. The first superficial dorsal constrictor is innervated by a branch of the second branchial nerve, Xth.

The Second Constrictor is inserted into the tip of the second epibranchial cartilage. Its fibres have a direction almost directly ventrad and laterad. Like the other three the muscle is wider at its origin than at its insertion.

Innervation.—A branch of the second branchial nerve.

The Third Constrictor is inserted into the tip of the third epibranchial. Its fibres have a general direction laterad, ventrad and caudad.

Innervation.—A branch of the second branchial nerve.

The Fourth Constrictor is inserted into the strong membrane which, attaching the third branchial arch to the body dorsally, forms the lateral part of the roof of the branchial chamber between the last arch and the trunk muscles. Its fibres have a general direction nearly horizontally rostrad.

Innervation.—This appears to be double. I find, as Norris describes, a twig from the second branchial nerve and also one from the large truncus intestio-accessorius as it curves ventrad beneath the muscle; Norris also describes this second motor twig.

The Levator Arcus Branchialium I (Fig. 84, L.a.b.).—So far as I can ascertain, the true character of this muscle has not previously been recognized. Apparently Wilder noted the muscle, for he writes that the first levator has a direction, in *Siren*, different from that of the rest, but that it had a much deeper origin and somewhat deeper insertion than the other muscles escaped his observation.

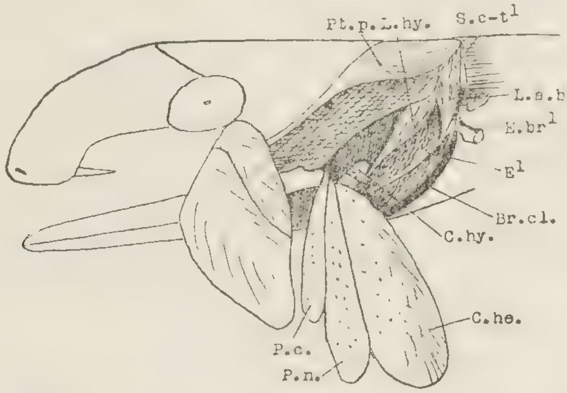


Fig. 84.—*Necturus.*—The same as Fig. 83, but with the Mm. depressor mandibulae and interhyoideus detached and turned down.

The muscle arises from the postero-internal and dorsal corner of the auditory capsule immediately medial to and above the uppermost corner of the origin of the pars cephalognathica, lateral to the posterior edge of the cranial origin of the first transverse spino-capitis muscle, under cover of the lateral margin of the first longitudinal dorsal myomere and the origin of the first superficial dorsal constrictor. The muscle is a relatively stout, short bundle of fibres roughly square in cross section; it arises by a very short flat tendon and swells very rapidly. The direction from its origin is caudad, laterad and ventrad deep to the upper end of the pars notognathica, and under this muscle it contracts again, its fibres being inserted into a narrow flat tendon which is inserted into the upper end of the anterior and external surface of the first epibranchial cartilage on a level with the top of the origin of the interhyoideus.

Innervation.—The ramus pre-trematicus of the IXth nerve passes laterad and ventrad deep to the muscle and sends several exceedingly fine fibrils into its deep surface; just where these end it was quite impossible to determine, they were much too fine to trace. The ramus post-trematicus winds caudad and laterad around its median and external surfaces and then passes ventrad across, superficial to the tendon of the muscle. The motor twigs to the muscle are given off as the nerve lies against the median surface.

The Interbranchial Muscles.—These are so essentially similar to those of the Axolotl that no further description is called for.

The several small muscles related to the outer ends of the epibranchial cartilages which were described by Wilder in *Siren* were not found in *Necturus.*

The subarcualia recti, including the first (cerato-hyoideus internus) are essentially similar to those of the Axolotl.

The Constrictor Pharyngei arises from the fascia dorsalis immediately behind, and in contact with, the fourth superficial dorsal constrictor, from the membrane into which that constrictor is inserted, immediately ventral to its line of insertion and from the third epibranchial cartilage.

There is little doubt that this extensive sheet represents the dorso-laryngeus and the third and fourth interbranchial muscles of Drüner. The insertion is into a mid-ventral raphe, and extends back so that the posterior fibres run directly transversely and ventrad from origin to insertion.

Innervation.—By twigs from the truncus intestio-accessorius of the Xth.

The Capiti Pectoral Muscles do not call for description; they are similar to those of the Axolotl.

5. Review of the Branchiate Amphibians.

Following the study of the anatomy and development of all the branchiate adult and larval amphibians except the Caecilians, a general survey seems desirable.

The next section of this paper will be devoted to the study of the adult anatomy of the Anura, Caducibranchiate Urodeles and the Caecilians. In these we shall have left behind most of those structures which, in tetrapods so far studied, have served us as identification marks whereby to determine homologies as between these and the fishes. So far we have been studying more or less fish-like animals, and in the Dipnoans and larval amphibians we believe we have identified, in much modified form, not a few of the primitive muscles of the elasmobranch fishes; most of these will later be found further modified in the abranchiate amphibians and the higher tetrapods.

Before passing to these more modified forms it is proposed to review again the muscles, and discuss the homologies adopted.

At the outset a general statement may be made, which applies to the arguments and evidence generally, in order to save repetition later.

Throughout the whole of this work it has been accepted as a fact that muscles which are innervated by the motor division of the same nerve are all of them to be regarded as having been developed from the primordial muscle plate of the segment to which that nerve belongs. There are, of course, exceptions to this generalization, and, where those exceptions are recognizable, they have been noted. In the great majority of instances the truth of the general proposition has been specifically demonstrated. So much is that so, that one has felt justified in assuming its truth in those instances where one met muscles whose homologies were to be determined, but whose development was not known in stages early enough to establish, beyond doubt, their segmental origin; the levator hyoidei of the anuran tadpole is an instance in illustration of this. In such cases, however, one has never had to rely only on the innervation of the muscle to determine its segmental origin. There has always been, in addition, the relation of the muscle to skeletal structures and/or a comparable muscle in one or more other forms to which one was able to appeal.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

On the ventrum of the head it has been found that the mandibular muscles of the primitive and larval amphibians are essentially similar to those of the fishes, and that there has been surprisingly little alteration in the muscles when compared, not with those of the bony fishes, but with the more primitive elasmobranchs. Already, in one or two of these, the ventral mandibular superficial constrictor showed a division into a submentalis and intermandibularis. It will be remembered that in not a few of the elasmobranchs this muscle, in its posterior portion, extended dorsally superficial to the ramus of the lower jaw. This condition was particularly noted by Lightoller, who designated it the Csv.1b or pars extramandibularis. There is no trace of any pars extramandibularis in the amphibians we have studied, nor, be it noted, was there in any one of the bony fishes.

Of the dorsal mandibular muscles of the elasmobranchs there apparently remain in the amphibians only derivatives of the mandibular adductors. The levator maxillae superior (L.1) and the first dorsal superficial constrictor (Csd.1) do not appear to have persisted in any form at all.* Lightoller is of the opinion that the L.1 persists as the pterygoideus muscle of tetrapods; this question has already been discussed, and it will be returned to after we have described the adult anatomy of the Amphibians.

---

* It may, however, be suggested that, since the extrinsic muscles of the eye-ball, levator bulbae and palpebral muscles, etc., are innervated by the Vth nerve, and by the mandibular ramus thereof, this is evidence that they are derivatives of the mandibular muscle plate. So far the argument is probably sound, but it might be further argued that their dorsal situation indicates that they may be regarded as derivatives of the missing dorsal muscles. This suggestion is tempting, but the question is complicated by the presence of both extrinsic eye muscles, and the two dorsal muscles in certain of the Selachians.

Further discussion of the rest of the derivatives of the adductor muscles of the primitive fishes is also reserved till later.

THE MUSCLES OF THE HYOID SEGMENT.

It will be remembered that in the elasmobranch fishes there were, in this segment, superficial dorsal and ventral constrictors, deep constrictors, dorsal (the interbranchial muscle, Csd.2a or pars quadrato-hyoidea of Lightoller) and ventral (the interhyoideus), and the levator hyoidei.

In the amphibians the hyoid muscles are depressor mandibulae, levator hyoidei, interhyoideus (the cerato-hyoideus externus) and the ventral superficial constrictor. In the Dipnoi there is, in addition, a dorsal superficial constrictor and a retractor mandibulae, the depressor mandibulae.

THE DEPRESSOR MANDIBULAE.

This muscle is of particular interest because it has generally been regarded as the forerunner of portion of the digastricus of the higher vertebrates. Lightoller has recently expressed the opinion that it is to be regarded as a composite muscle developed from the pars quadrato-hyoidea and the levator hyoidei, the pars cephalognathica being derived from the levator hyoidei and the pars notognathica from the pars quadrato-hyoidea; a somewhat similar, but not so explicitly expressed, opinion was held by Drüner and by Gaupp.

It appears, however, that the pars cephalognathica may, itself, be a composite muscle.

Lightoller's conclusions were founded on a study of the muscles of the Axolotl and adult *Megalobatrachus*, in neither of which has any levator hyoidei been preserved. It would appear that he was unaware of the fact that a levator was present in some, at least, of the perennibranchiate urodeles, and, so far as I am aware, there had been at that time no record of its transient development in the anuran tadpole; I believe that my discovery of this muscle is a definite contribution to the subject; I can find no previous mention of the muscle.*

There appears no reason to doubt that I have correctly identified this little muscle, although I have not been able to trace it back to the stage where it is separated from a primordial hyoid muscle plate. It is very clearly innervated by the VIIth nerve and is attached on the one hand to the skull and on the other to the upper end of the ceratohyal. Further, there is a veritable levator hyoidei developed in *Siren* and in *Necturus*.

It can be stated quite confidently that the levator hyoidei of the anuran tadpole is a caducous muscle and that it takes no part in the formation of the depressor mandibulae in the Anura. I have been able to observe the development of the one and the gradual disappearance of the other, and at no time does the posterior margin of the depressor come into contact with any portion of the levator; there is always a considerable gap between the two muscles.

On the other hand, I have observed in the 13–14 mm. larva of the Axolotl (*Amblystoma tigrinum*) that a few of the deeper fibres of the pars cephalognathica of the depressor are inserted into the tip of the ceratohyal. These few fibres may be regarded as a very transient levator hyoidei, but the pars cephalognathica is at this stage a well developed muscle, and these few fibres form but a very small portion of the whole.

In *Necturus*, and presumably also in *Siren*, the levator hyoidei is related to the pars cephalognathica precisely as this little transient muscle is to the larger in the larval Axolotl, and the two muscles are innervated by twigs of the one branch of the VIIth nerve. In *Necturus*, however, the levator maintains its identity throughout life, its tendon being bound to that of the cephalic head of the depressor.

There is no levator hyoidei in the adult Anura, nor, so far as is known at present, in the adult caducibranchiate and cryptobranchiate urodeles.

But if the levator is not a contributor to the cephalic head of the depressor mandibulae in the Anura, whence comes the definite duality of the depressor?

Since the muscle is very evidently not developed from the levator in these amphibians it is to them one must look for the explanation of a duality of constitution which is exhibited in all amphibians, but which in some other forms appears conceivably due to the incorporation of the levators. Since the duality is clearly not due to the incorporation of the levator in the Anura it is probably not due to that factor in those other forms.

---

* Edgeworth (1935, Figs. 417 and 419) reproduces two drawings from Luther in which this muscle is shown and designated Suspensorio-hyoideus.

It will be remembered that in the anuran tadpole the pars notognathica arises from the lateral end of the anterior edge of the ceratohyal and that this origin persists until, at metamorphosis, the ceratohyal becomes converted into the stylohyal.

Also it will be remembered that in the 13–14 mm. larvae of the Axolotl, this head of the depressor was very much smaller than the cephalic head and took its origin from the ceratohyal immediately behind the posterior end of Meckel's cartilage.

Now it will also be remembered that in the Dipneumona there is a retractor mandibulae which is formed from the middle portion of the hyoid muscle plate. Edgeworth's description of the development of this muscle has already been quoted. It is attached, in front of the dorsal portion of the constrictor sheet, to the auditory capsule.

Edgeworth quite definitely states that this retractor is not homologous with the depressor mandibulae of the amphibia. With this statement I find myself unable to agree, in view of the fact that in the Anura, at least, the depressor is certainly not homologous, as he states, with the levator hyoidei.

To my mind we have here the explanation we seek. To me it seems that the pars cephalognathica may be homologized with this retractor of the dipneumonous dipnoans, and perhaps with those lateral fibres of the interhyoideus of *Neoceratodus* which arise from the mandible.

It further seems probable that this muscle is homologous with the pars quadrato-hyoidea of the elasmobranchs. It was pointed out, when reviewing this muscle in the section describing the selachian muscles, that the anterior part of the dorsal superficial sheet in the hyoid segment was probably really the deep constrictor forced to the surface by changes in the visceral skeleton in its own segment and in that in front. In any case the pars quadrato-hyoidea is the most anterior portion of the hyoid sheet, and it is just this portion which gives rise to the retractor mandibulae of the dipnoans; the posterior portion forms an interrupted dorso-ventral sheet behind it.

This homology, however, in view of the evidence, cannot be regarded as excluding the possibility of the hyoid levator being a contributor to the cephalic head of the depressor in tetrapoda other than the Anura. It is possible that in these last the articulation of the ceratohyal to the meta-pterygoid, by divorcing the levator from the rest of the muscle, introduced a peculiarity into the history of these muscles which is not present in other tetrapods, in none of which does the articulation of the ceratohyal and the suspensorium occur.

The origin of the posterior part of the depressor from the ceratohyal in its early stages is of importance in determining its homology. It is noteworthy that in the youngest Axolotls which it was found possible to dissect, it was not possible to demonstrate the muscle at all; when first it appeared it was a very narrow muscle immediately behind the jaw. As the dorsal portion of the Csv.2b grew smaller and smaller, this muscle increased in bulk. One gained the definite opinion that this posterior head of the depressor was developed by the transfer of the dorsal fibres of the constrictor sheet to the mandible. Druner was of the opinion that the depressor could be divided into a deep layer derived from the hyoid levator and a more superficial layer which he derived from the cerato-hyoideus externus. It is possible that he observed the apparent decrease in size of this last muscle, which takes place as the dorsal fibres of the more superficial constrictor are transferred to the posterior end of the mandible, and concluded that it was an actual reduction of the cerato-hyoideus which he observed. In my experience the interhyoideus muscle of the amphibian is never caducous.

It is now suggested that the pars notognathica of the depressor mandibulae is derived from the remainder of the dorsal portion of the superficial hyoid constrictor, the partes interinscriptionalis and arcuata.

The phylogenetic history of the depressor mandibulae, under this interpretation, may be regarded as being presented in two stages in the amphibians.

Stage one is the dipnoan, in which the anterior, deeper, fibres of the dorsal constrictor, the pars quadrato-hyoidea, are modified to act as a retractor mandibulae, thus forming the primitive pars cephalognathica.

Stage two is the more advanced, amphibian, in which the remaining fibres of the dorsal constrictor are transferred inferiorly to an insertion on the end of the mandible and form the pars notognathica.

Finally, it is not improbable that the levator hyoidei, which appears to have been lost entirely by the abranchiate amphibians, may also be incorporated in the pars cephalognathica, in forms other than the Anura.

Edgeworth states that in certain Anura (and *Lepus*) the lower end of the hyoid myotome, after its separation from the interhyoideus, becomes separated from the part above to form a hyomaxillaris muscle which, later, gives rise to the inner portion (cephalic head ?) of the depressor mandibulae. He further states that in the urodeles, *Necturus* and *Triton*, a corresponding anlage develops into a hyomaxillaris ligament and that in the Selachii no hyomaxillaris anlage is formed (1911, pp. 213–220).

Clearly there is some confusion here ; to begin with, whereas there is a strong hyomaxillaris ligament in the Axolotl, such a ligament in *Necturus*, and presumably in *Siren*, is represented by the conjoined tendons of the levator hyoidei and of the pars cephalognathica and, moreover, there is a well-defined and relatively large levator hyoidei muscle developed in these two genera. One is compelled to assume that the levator in the Urodela was developed from a hyomaxillaris anlage, as in the Anura.

My own study of the development of the depressor leads to the belief that both parts are developed from anterior and dorsal portions of the hyoid myotome. At their first appearance in the youngest urodele larvae I have been able to recognize them in, there has been a well developed Csv.2b extending dorsally behind them. Further than this in these forms there has been a well developed Csv.2a ventral and medial to the two parts of the depressor.

The lower end of the hyoid myotome would be the mid-ventral portion, or the forerunner of this, and the presence of perfectly typical Csv.2a and b surely indicates that it was not this portion of the hyoid myotome which gave rise to the depressor in the amphibians.

Apparently that which Edgeworth describes was in reality the lower and anterior portion of the dorsal part of the hyoid myotome ; maybe Edgeworth refers to the Csv.2 under the name of "interhyoideus ".

Schultze describes five muscles in the upper part of the hyoid segment in anuran tadpoles which he studied.

Their synonymy is as follows :

Schultze.	This work.		
Orbito hyoideus	Dilator hyoidei		
Suspensorio-hyoideus	Levator hyoidei		
Cerato-hyo-angularis	Pars notognathica		Depressor mandibulae
Suspensorio-angularis	Pars notognathica		
Quadrato-angularis	Massetericus (tadpole)		
	Masseter	major minor minimus	Adult

The Interhyoideus and the Superficial Ventral Constrictor.

The ventral superficial hyoid constrictor sheet in the amphibians has been designated interhyoideus, subhyoideus, cephalo-dorso-pectoralis, sphincter colli, posterior intermandibular, and posterior mylohyoid muscle by different writers. The interhyoideus has been fairly constantly designated cerato-hyoideus externus.

Lightoller has homologized the anterior portion of the Csv.2 with the interhyoideus of the selachians, and the posterior portion he regards as the homologue of the pars inscriptionalis of the hyoid superficial ventral constrictor, and there is no doubt that there is strong evidence in support of such a view.

The anterior part of the Csv.2 in the urodeles arises on each side from the ceratohyal and the fibres are inserted into a mid-ventral raphe deep to the Csv.1 precisely as is the interhyoideus in the selachians. Not only is this so, but in the Anura the only superficial ventral constrictor is certainly developed from a muscle which arises on each side from the ceratohyal and is inserted into a mid-ventral raphe, is in fact developed from a veritable interhyoideus.

These facts would seem to settle the question quite satisfactorily ; but doubt is introduced by the presence of the so-called cerato-hyoideus externus. This muscle is very definitely developed from the deep surface of the anterior portion of the ventral hyoid plate, as also is the interhyoideus, not only in the selachians, but also in the teleosts. There is little room for doubt that it is the interhyoideus which, in the teleosts, contributes the hyoid component to the protractor hyoidei. This lies deeply to the rest of the ventral constrictor derivatives and its fibres have a nearly longitudinal direction, similar to that of the cerato-hyoideus externus.

It is demonstrable, then, that the interhyoideus muscle of the selachians was capable of being modified so that its fibres have a nearly longitudinal direction, and its insertion transferred from the deep surface of the Csv.2 to deeper structures. These modifications have taken place in the teleosts.

It appears, therefore, that one must conclude that the cerato-hyoideus externus is homologous with the interhyoideus of the selachians.

The alternative is to regard this amphibian muscle as a quite new muscle, and to this one might be persuaded by the insertion of the anterior portion of the Csv.2a deep to the Csv.1b. In this connection it may be pointed out that the posterior portion of the Csv.1b (Csv.$1b^2$) is itself inserted deep to the anterior portion (Csv.$1b^1$) of the same muscle in the frogs.

In the Dipnoi there is an interhyoideus muscle deep to the superficial hyoid constrictor, but there is no cerato-hyoideus externus.

Having in mind the fact that the Csv.2 of the perennibranchiate urodeles extends right back to the posterior margin of the opercular fold, it seems that this extensive sheet may be regarded as homologous with the partes interinscriptionalis and arcuata of the selachians.

In the Anura there is no cerato-hyoideus externus. The interhyoideus has been modified to act as a Csv.2.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

In the selachians the muscles of these segments were superficial dorsal and ventral constrictors, interbranchial muscles, levators, epibranchial spinal muscles, epiarcualia obliqui, adductores arcuum branchialium and coraco-branchiales.

In the amphibians generally, the following are seen: superficial dorsal constrictors, interbranchiales, subarcualia transversi, obliqui and recti; in particular groups there are also one single branchial levator, a single coraco-branchialis, and possibly a ventral superficial constrictor sheet.

THE SUPERFICIAL DORSAL CONSTRICTORS AND THE BRANCHIAL LEVATOR.

The discovery of a veritable branchial levator in *Necturus* may be regarded as providing partial confirmation of the identification of the so-called levators of the amphibians as the homologues of the superficial dorsal constrictors.

These muscles are four in number in every branchiate amphibian that has yet been studied. They arise from the fascia dorsalis and are inserted into the subcutaneous fascia close to the upper ends of the epibranchial arches. Both at their origin and at their insertion they are definitely more superficially placed than are musculi marginales, and these latter are, apparently beyond question, homologous with the deep constrictors of the branchial segments in the selachians. In the selachians the levators are more deeply placed than the deep constrictors. When to these facts is added the discovery of a branchial levator in just precisely the situation of the levators in the Dipnoi and in the teleosts it would appear that we must conclude that, except for this single levator, those muscles are not developed in any of the amphibians except the Dipnoi. In these latter all five levators are developed, and they are deeply placed, as in the teleosts and as in the elasmobranchs. It should be particularly noted that in the dipnoans the musculi marginales are continued dorsad to insertions on to the cartilaginous roof of the branchiopharynx, and that the levators are placed, each of them, deep to its own segmental M. marginalis.

THE VENTRAL BRANCHIAL MUSCLES.

The various accounts which have been published describing the development of these muscles are conflicting, and none of them agree with my own findings, so that their development is still far from being properly understood.

It appears quite clear that the primordial branchial muscle plates divide into dorsal, middle and ventral portions in the amphibians as in the selachians. It is further clear that the dorsal portion gives rise only to the superficial constrictors (levators), that the middle portion gives rise only to the Mm. marginales, and that from the ventral portion there are developed the various ventral muscles.

The superficial constrictors in *Amblystoma* very certainly give rise, at metamorphosis, to an anterior portion of the cucullaris.

The Mm. marginales in all forms are completely caducous.

The fate of the superficial constrictors in the Anura is not so clear.

In the fourth branchial segment there is no M. marginalis developed in any of the amphibians which has yet been studied.

In well advanced tadpoles of various anuran species I find the following muscles : superficial dorsal branchial constrictors (the so-called levators), constrictor pharyngei, omo-hyoideus, cucullaris, dorso-laryngeus, cranio-hyoideus and cranio-laryngeus.

Of the superficial constrictors there are quite certainly three, and, it may be, four. There are no other muscles present which could possibly be interpreted as " levators ".

Edgeworth (1911, p. 247) says that on the atrophy of the cerato-branchialis (subarcualis rectus I of this work) and Mm. marginales, all four levators extend downwards, and their lower ends become attached to the body and processus posterior medius of the hyoid bar.

Now, in the anura which I have studied the four muscles which are attached below as just described are the constrictor pharyngei (petrohyoidei anterior), dorso-laryngeus, cranio-hyoideus and cranio-laryngeus (petrohyoidei posteriores), and these are fully developed whilst still three, at least, of the constrictors are short muscles, and are not in any way changed from their early form. Later these short muscles disappear without, apparently, contributing to the formation of any other muscles whatsoever.

Edgeworth (l.c.) further says that in the 12 mm. larva of *Rana* there is a downgrowth of the fourth levator forming the diaphragmato-branchialis lateralis of Schultze. Its upper end, he says, becomes attached to the fourth bar, its lower end to the diaphragm, and that the cucullaris is formed early in metamorphosis from cells proliferated from the outer surface of this levator.

I find the cucullaris quite extensively developed in tadpoles long before the development of the pectoral girdle or fore limbs, and in slightly later stages a muscle, which subsequently proves to be the omo-hyoideus, having just the attachments of the diaphragmato-branchialis lateralis of Schultze.

It is possible that both these muscles are derived from the upper end of the fourth branchial muscle plate.

The insertion of the constrictor pharyngei into the mid-ventral raphe and its situation immediately behind the fourth branchial arch leads one to identify it as the fourth subarcualis transversus with some confidence, notwithstanding the fact that one has been able to observe it to grow downward from above. It may be suggested that there is incorporated with it the missing fourth M. marginalis, and that there has been no splitting off of the ventral moiety, which in the other segments gave rise to the ventral muscles, so that in consequence the composite muscle had to grow down to reach the mid-ventral raphe.

There is no muscle reaching the mid-ventral line behind this in the Anura.

Drüner was of the opinion that in the Urodeles an atrophied fifth branchial segment is present, and represented by nerve rami and muscles, behind the fourth. One notes, in conformity with this suggestion, that in the urodeles, *Necturus*, and the Axolotl, the muscle sheet which occupies the situation of the constrictor pharyngei of the Anura is much more extensive.

It seems probable that the three posterior petrohyoid muscles of the Anura are modified derivatives of this fifth segment, and that one of them represents the dorso-laryngeus of the urodeles.

The history of the omo-hyoideus is of particular interest. There is little doubt that, in its anterior part, which appears first, it is a derivative of one of the branchial muscle plates. Its innervation in the adult by the first and/or second spinal nerve by way of the hypoglossal nerve, is therefore a definite instance of the capture of a Xth nerve muscle by one of the spinal nerves.

THE CEPHALIC MUSCLES OF THE ABRANCHIATE AMPHIBIANS.

It is now proposed to review the adult anatomy of the various groups of the Amphibia, excluding the perennibranchiate forms.

In all these the branchial skeleton has given place to the " hyoid " skeleton which, variously modified, acts as the support of the tongue throughout the higher vertebrata. This profound modification of the visceral skeleton has naturally been accompanied by equally profound modifications of the musculature, whose inception has already been studied in the branchiate larvae and adult amphibians.

Together with those which have just been studied, the further modifications which will be met with constitute the connecting links between the primitive musculature of the fishes and that of the tetrapods, and their comprehension is a necessary prelude to the proper understanding of the cephalic musculature of the reptiles and the mammals.

1. The Adult Caducibranciate Urodeles.

The Adult Amblystoma.

(Fig. 85.*)

MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a and b are similar to the muscles in the Axolotl as also are the muscles of mastication; so much is this so that no further description is called for.

MUSCLES OF THE HYOID SEGMENT.

The Csv.2a and b are essentially as in the Axolotl. The ceratohyal has lost its connection anteriorly and medially with the rest of the hyoid skeleton. It is now an elongated spathulate cartilage with a curved cylindrical posterior end. This cylindrical portion curves dorsad behind the end of the mandible and, at its tip, is attached to the hinder margin of the auditory capsule behind, and somewhat higher than, the mandible. The Csv.2a arises from the dorsal surface of this short posterior cylindrical section of the ceratohyal. The Csv.2b arises from the outer surface of the depressor mandibulae. Actually its origin is from a strong fascia, covering this muscle, which is bound in front to the fibrous capsule of the maxillo-mandibular joint and behind to the pectoral girdle. The greater part of the fibres of the Csv.2b converge to be inserted just behind the jaw joint.

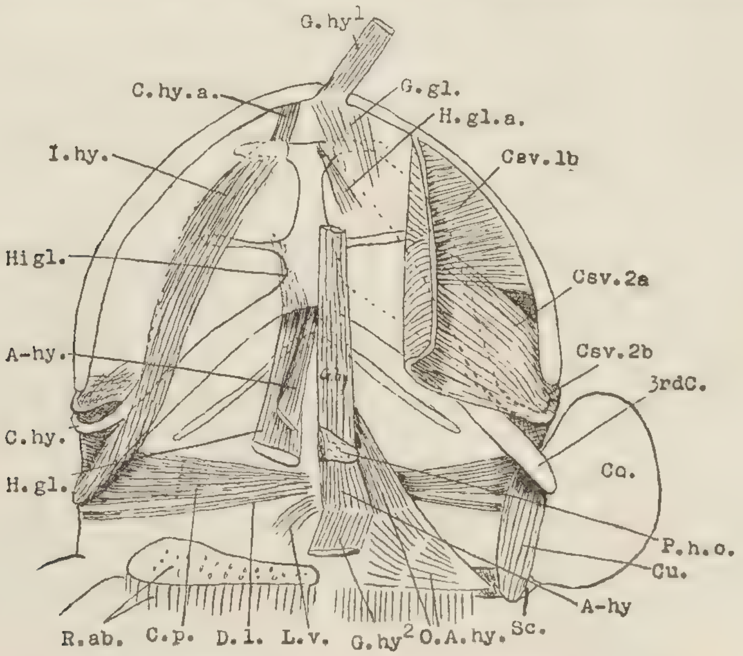


Fig. 85.—*Amblystoma.* The muscles of the ventrum of the head.

The Pars Cephalognathica of the depressor mandibulae is similar to that of the Axolotl. The Pars Notognathica is more extensive, and the two parts together now occupy most of the position of the superficially placed upper end of the interhyoideus and the superficial constrictors, arising from the fascia dorsalis. This statement, it should be understood, is relative for, to judge by the specimens at my disposal, there has been an actual condensation of structures in this area so that the posterior end of the jaw is brought actually nearer the pectoral girdle and there is much less dorsi-ventral depth.

---

* Fig. 85 is a slightly schematic illustration of the ventral musculature of *Amblystoma.* Besides the muscles described in the text, the following structures are shown. The hyoid skeleton, 3rd C, its third cornu. The post-hyoid ossicle, P-h.o., the coracoid of the left side turned away outward, Co., the lower end of the scapula, Sc., the anterior end of the rectus abdominis muscles, R.ab., the dorsal end of the ceratohyal cartilage curling to its attachment to the back of the skull, C.hy. The anterior end of the hyo-glossus muscle is represented as seen through the hyoid plate and cornua; these latter are indicated, where they are dorsal to the muscles, by dotted outlines.

The Interhyoideus (Fig. 85, I.hy.) now arises from the tip of the third process of the hyoid plate. This is the longest of the four lateral processes; its dorsal end lies above and behind the point of attachment of the stylohyal to the skull. The origin of the interhyoideus is wrapped right around this cartilage, but the fibres curve so that they come to lie ventral to and in front of the cartilage between it and the upper end of the flattened portion of the ceratohyal. The muscle follows down the direction of the third process till it comes to lie a little distance medial to the posterior end of the jaw, where it turns more directly forward and gains the ventral surface of the ceratohyal at about the middle of its length. It is inserted on to the anterior one-third of the length of this surface. The ceratohyal lies dorsal to the third process behind the jaw above, and below this it lies anterior.

Whether the Cerato-hyoideus anterior (Fig. 85, C.hy.a.), a tiny muscle which joins the anterior tip of the ceratohyal to the ramus of the jaw just to one side of the submentalis, is a mandibular, hyoid or hypobranchial spinal muscle cannot be stated. Nothing is known of its innervation or development beyond the fact that, like the genioglossus of the Anura, it first makes its appearance independently of any muscle except for its proximity to the submentalis; it may be a portion of the genio-glossus.

No levator hyoidei is to be found; this was, of course, not expected to be found.

MUSCLES DERIVED FROM THE BRANCHIAL MUSCLE PLATES.

Drüner found in the adult *Amblystoma* a cerato-hyoideus internus, interbranchiales 4 and 5, dorso-laryngeus, levatores arcuum branchialium 1, 2, 3 and 4, and a laryngeus ventralis.

In the specimens at my disposal no muscle was found which could be identified as a cerato-hyoideus internus.

Interbranchiales 4 and 5 and the dorso-laryngeus have been, it is believed, identified, as also the "levatores arcuum branchialium". Notwithstanding this agreement in the number of the muscles it will be found that my description is radically different from that of Drüner.

The superficial dorsal constrictors (levators of Drüner) are believed to have given rise to a cephalic head of the cucullaris. This muscle, it will be remembered, arose from the fascia dorsalis behind the dorso-laryngeus and with its anterior dorsal corner deep to that muscle; this was the condition in the Axolotl. In *Necturus* the superficial dorsal constrictors were found to constitute an almost continuous sheet whose anterior part arises immediately above the pars cephalognathica of the depressor mandibulae, and whose posterior margin is so closely related to the anterior margin of the cucullaris that one has to dissect carefully to separate the two muscles. The dorso-laryngeus is situated superficially to this closely knit portion of both muscles. In both *Necturus* and the Axolotl the anterior boundary of the cucullaris is just at the posterior boundary of the superficial constrictors.

In the adult *Amblystoma*, the cucullaris (Fig. 85, Cu.) arises from a line which is precisely that of the origin of the superficial constrictors in the Axolotl and in *Necturus*, as well as from an origin which is similar to the origin of the cucullaris in those forms. It is nearly three times as wide at its origin as the muscle in the larva and in the other form.

This cucullaris of the adult *Amblystoma* separates itself into two portions as one liberates it from its insertion. The anterior portion is that which arises from the line of origin of the constrictors. This separation into anterior and posterior parts takes place, in every specimen dissected, at the same line and extends down almost to the insertion of the muscle.

It is concluded that as the branchial slit is closed and as the branchial arches are metamorphosed into the hyoid skeleton the constrictors grew down along the branchio-pectoral membrane to a new insertion on to the scapula along with the cucullaris.

Innervation.—Though I cannot state it as a fact, I believe that this interpretation of the origin of the cephalic head of the cucullaris is further supported by its innervation. I find three nerves entering the deep surface of the muscle. Two of these come from a nerve which is believed to join the ramus intestino-accessorius just after its emergence from among the other branches of the IX-X nerve complex. The nerve is very fine and I was unable to trace it in any dissection without breaking it.

The Dorso-laryngeus (Fig. 85, D.l.) and the Constrictor pharyngei (C.p.) present quite altered outlines. In the Axolotl these muscles together formed, on each side, a triangular sheet with its apex at the origin of the dorso-laryngeus and its base at the mid-line beneath the pharynx. In the adult this outline has been reversed, the apex now lies immediately ventral to the larynx, where the posterior boundary of the larval muscles was, and the base extends from the point of origin of the dorso-laryngeus forward, superficially to the cucullaris, along the same line of origin, but not extending quite so far forward.

Along this line of origin one finds a variable number, four to seven, of groups of fine strands of fasciculi which pass ventrad and mediad deep to the upper end of the interhyoideus. These reach the ventral surface of the pharyngeal mucosa behind the posterior cornua of the hyoid. Close to this point they are inserted into a transverse intersection, the posterior group alone not being interrupted by the intersection. Contracted to a narrow ribbon they then pass directly across to be inserted ventrally to the larynx.

The posterior, uninterrupted, group is constantly present ; it arises in the position of the M. dorso-laryngeus of the Axolotl. This strand, right from origin to insertion, is separated from the rest by a constant small interval ; it is believed to be the M. dorso-laryngeus.

The remainder of this narrow sheet of muscle fibres is homologized with the M. constrictor pharyngei of the Axolotl. The origin has been transferred from the last branchial cartilage to a higher fixed point. Whilst thus gaining in length, the muscle has lost in width.

Actually the transfer has not involved more than a short migration of the dorsal ends of the fibres. Quite a short forward rotation, with some dorsal movement, brings the point of origin in the Axolotl to the position of that in the adult.

The dorso-laryngeus is inserted on either side of the larynx, the constrictor pharyngei, just in front of it.

Immediately behind the insertion of the M. dorso-laryngeus there is a short laryngeus ventralis muscle (Fig. 85, L.v.). The fibres of this muscle arise from the submucosa behind the larynx and curve rostrad and mediad to an insertion on each side of the posterior half of the length of the slit-like closed larynx.

Innervation.—This is from the truncus intestino-accessorius X.

It seems possible that Drüner's description of the muscles of the adult *Amblystoma* really applies to some other amphibian. Naturally I have been puzzled by the marked differences in our two findings. To test the correctness of my own I have cleaned these muscles very completely, working under a relatively high power of the Greenough dissecting microscope ; I have then carefully liberated them from their origins on both sides and have cut away the whole thickness of the pharyngeal ventral floor, from in front of the larynx to behind the posterior limit of the laryngeus ventralis, removing the muscles and larynx intact. The preparation was then lightly stained with borax-carmine and studied after clearing in Spalteholz solution.

The above interpretation of the origin of the cephalic head of the cucullaris muscle and its situation deep to the origin of muscles which must be regarded as derivatives of muscle primordia more deeply placed than the superficial dorsal branchial constrictors once more raises the question as to whether, after all, it would not be better, and more correct, to regard these last as levators.

It is admitted that their situation in the adult, deep to the constrictor pharyngei and dorso-laryngeus, is contrary to that which should have been expected. On the other hand, in the larva the dorso-laryngeus lies superficially to the trapezius at its origin.

Now, according to Edgeworth, the cucullaris is developed from one or more primordia split off from the dorsal ends of the branchial muscle plates medial, that is deep, to the portions which give rise to the superficial muscles. Volker, according to Addens (1928), has shown that in *Larus ridibundus* the cucullaris is developed from split-off portions of the occipital myomeres. It may be remembered that Edgeworth has already been quoted as stating specifically that the cucullaris of *Rana* is developed early in metamorphosis from cells proliferated from the outer surface of the fourth levator.

All these descriptions of the development of the cucullaris ascribe its origin to primordia more superficially placed than that of the dorso-laryngeus, which, however, is found superficially to it. The dorso-laryngeus is unquestionably a deep constrictor.

Although the evidence is conflicting, and far from conclusive, I find, after my study of the structures themselves, that the so-called " levators " of the amphibians appear to me to be superficial muscles.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The genio-hyoideus muscle (Fig. 85, G.hy.) has increased in width and slightly in thickness, otherwise it is as in the Axolotl.

The claviculo-hyoideus is now quite clearly differentiated into three separate muscles, the hyo-abdominis, the hyoglossus, and the omo-abdomino-hyoideus.

Upon removal of the genio-hyoideus the last two muscles are brought into sight, the last being superficial to the lateral portion of the hyo-glossus.

The Omo-abdomino-hyoideus (Fig. 85, O.A.hy.) arises from the third hyoid cornu close to its attachment to the basihyal plate. At its origin it is a relatively thick muscle with an oval cross section. The medial fibres pass directly caudad to be inserted into the first tendinous inscription of the rectus abdominis, the lateral fibres swing laterally and caudad to be inserted into the scapula just laterally to the glenoid cavity. The intermediate fibres radiate between these two insertions. In similar manner the fibres which are attached to the scapula radiate widely, the most posterior pass directly mediad and ventrad to the first inscription, the rest having intermediate directions. When this muscle is dissected free and examined by transmitted light, a tendinous inscription is found running transversely across it just where the narrow anterior portion definitely commences to widen out, and another inscription, which passes obliquely from behind forward and laterad, commencing at the lower end of the inscription of the rectus abdominis and ending a short distance behind the lateral end of the first. Whilst these suggest a duality of origin for the muscle—cephalic and spinal, similar to that of the omo-hyoideus of the Anura—since nothing is known of the early history of the muscle, one can but mention this possibility. The muscle is fairly certainly homologous with part, at least, of the omo-hyoideus of the Frog.

The Hyo-glossus (Fig. 85, H.gl.) muscle arises actually as the anterior continuation of the rectus abdominis ; it comes forward on each side of the pericardium. As it reaches the anterior limit of the pericardium, its strands become gathered together to form a relatively stout rounded muscle. This continues forward under cover of the genio-glossus and medially to the omo-abdomino-hyoideus. Alongside of the origin of this last muscle, the hyoglossus passes forward dorsally to the inner end of the third cornu and ends by being inserted into the connective tissue of the tongue just above the second cornu.

The Abdomino-hyoideus (Fig. 85, A-hy.) arises as the forward continuation of the middle strip of the rectus abdominis. The two muscles lie side by side dorsally to the posterior end of the genio-hyoidei. They are short flattened muscles which are inserted into the posterior edge and ventral surface of the post-hyoid ossicle.*

The Genio-glossus (Fig. 86, G.gl.) is a very thin sheet of muscle fibres which arise from the inner surface of the mandible, close to the upper edge, for a short distance on each side of the symphysis and extend directly caudad, to end in the tissues of the tongue.

The Hyo-glossus Anterior (Fig. 86, H.gl.a.) arises by a very fine short tendon from the anterior edge of the hyoid plate. The two muscles arise almost together at the mid-line. The fibres pass caudad and laterad and terminate in the substance of the tongue.

Innervation.—All the hypobranchial spinal muscles are innervated by the hypobranchial nerve from the Ist and IInd spinal nerves.

Plethodon and *Diemyctylus.*

(Fig. 86.)

Of these genera I had for dissection two specimens each of *P. glutinosus* and *D. viridescens.* All four specimens were in an excellent state of preservation, and permitted the dissection of the muscles without difficulty. They were, however, all small and one was not able to determine the innervation of most of the muscles.

The two genera are described together because they are so essentially similar. *Plethodon* is one of the Lechriodont salamandrine urodeles and, therefore, closely allied to *Amblystoma* ; while *Diemyctylus* is one of the Mecodonta, also a salamandrine. It is therefore somewhat surprising to find that the former should so closely resemble the latter in its cephalic musculature, and differ in quite important details from the more closely allied *Amblystoma.*

---

* The post-hyoid ossicle is a small triangular plate of bone developed from the posterior end and cornua of the basibranchial cartilage of the Axolotl. Into its two anterior edges the genio-hyoideus is inserted into its base, that posterior continuation of these muscles which is inserted into the tendinous inscription of the rectus abdominis. The ossicle is bound in its place only by the muscles which are attached to it.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Submentalis (Csv.1a).—Abnormal in both forms, this muscle is better developed in *Plethodon* than in the other genus. It is represented by two small flat sheets of fibres, one on each side of the symphysis menti. Each arises from the subdermal, inferior, surface of the mandible, and its fibres pass caudad and mediad to be inserted into a delicate membrane. This membrane is but ill differentiated from the deeper connective tissues anteriorly, but becomes quite definite between the median ends of the ventral superficial constrictor muscles behind the Csv.1a.

The Intermandibularis muscle (Csv.1b) is divided into anterior and posterior portions, in *Plethodon*, by a small triangular gap. This division is not present in *Diemyctylus*.

The muscle arises from the median surface of the mandible a short distance above the ventral edge. The line of origin commences a short distance posteriorly to the posterior margin of the submentalis and extends back to an equal distance anterior to the jaw joint. The anterior fibres are transverse in direction and, in *Plethodon*, a few of these are apparently araphic. In *Diemyctylus* none reaches the mid-line, all being inserted into a narrow median raphe. The posterior fibres are inclined caudad. In *Plethodon* the fibres are of varying length (see Fig. 86) and the very delicate raphe is so transparent that the genio-hyoid muscle is seen through it quite clearly. The membrane is, however, here quite unattached to the deeper structures. When the muscles of one side are detached from their origin it is found that one can reflect the other set, without rupturing any connections, by turning the freed set back across the mid-line.

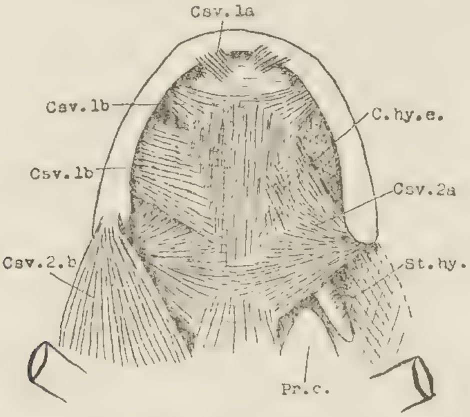


Fig. 86.—*Plethodon.* The muscles of the ventrum of the head.

It is to be particularly noted in this connection that the underlying anterior portion of the Csv.2a is not attached to this median raphe in either of the genera.

Innervation.—It is quite impossible to speak positively on this. One can only record that fibres of the Vth nerve alone were found related to the muscles.

Muscles of Mastication.

There are present here the same three muscles as in *Amblystoma.* Except that they are, relatively, smaller than in that genus no differences worthy of note were observed.

MUSCLES OF THE HYOID SEGMENT.

The Csv.2a arises from the posterior margin of the quadrate immediately beneath the depressor mandibulae muscle. From this origin the fibres pass mediad, radiating rostrad and caudad, with the middle fibres of the muscle directly transverse in direction. The most anterior fibres run forward nearly parallel with the ramus of the jaw and extend a long way forward beneath the Csv.1b. The most posterior fibres trend caudad some distance and, in *Plethodon,* lie deep to the Csv.2b at their origin and for a little part of their length.

The Csv.2b arises by a narrow, short and strong band of ligament from the lateral and inferior surface of the mandible at and behind the joint. From this origin the fibres radiate caudad. The most medial fibres pass caudad and mediad, the most lateral more directly caudad, in *Plethodon*. The muscle is better developed and larger than in the other genus and its thickened medial margin lies superficially to the posterior fibres of the Csv.2a, whilst its more lateral fibres have a direction directly caudad. In *Diemyctylus* the medial margin of the muscle lies posteriorly to the posterior fibres of the Csv.2a. Medially the two portions of the muscle form a continuous sheet of fibres. Laterally, near the origin of the two portions, there is a small gap between them. The most lateral fibres have a mediad trend so that their insertion lies medially to the shoulder joint, instead of, as in *Plethodon*, laterally thereto.

The insertion of the muscle is into a sheet of membrane which lies, subdermally, over the anterior portions of the shoulder girdle.

Innervation.—A twig of the VIIth was the only nerve observed related to either part of the muscle.

The resemblance of the Csv.2b to that of *Ichthyophis* is very close, whilst the condition in *Diemyctylus*, in which Csv.2a and b form a continuous sheet on either side of the mid-line, is intermediate between the condition of the muscle in *Plethodon*, *Amblystoma*, and *Notophthalamus*.

The Cerato-hyoideus externus (interhyoideus muscle) is present in both genera, and may be seen in *Plethodon*, through the membrane into which the Csv.2a is inserted, medial to the anterior part of the Csv.2a.

The Depressor mandibulae in both forms is a small muscle which arises from the squamosal and posterior superior area of the skull. Whilst no actual separation into partes cephalo- and noto-gnathica is visible, it was found that, in both forms, the muscle separated cleanly into a smaller, anterior and deep, and posterior, more superficial, portion. There appears no reason to doubt that these are the two "partes" of the muscle which have been found so well differentiated in other amphibians.

MUSCLES OF THE BRANCHIAL SEGMENTS AND THE HYPOBRANCHIAL SPINAL MUSCLES.

Whilst these present some departures from the types already described, they are not of a kind or degree to call for detailed description.

Molge. (s. *Notophthalamus.*)

Material.—A single specimen of *M. torosus*, excellently preserved, which was received from the American Museum of Natural History.

MUSCLES OF THE MANDIBULAR SEGMENT.

There is no M. submentalis.

The Intermandibularis muscle arises from the anterior half of the inner surface of each mandible and meets its fellow in the mid-ventral raphe. The fibres are directly transverse.

The muscles of mastication are sharply divided into pterygoideus and temporalis.

The Pterygoideus is very imperfectly divided into partes posterior, anterior, and internus. The pars posterior arises from the mid-dorsal intermuscular septum above the posterior end of the skull and for a little distance beyond it posteriorly. The extreme posterior tip of the muscle is very narrow and it lies medially to the anterior end of the longissimus dorsi muscle of its own side. Passing forward, the muscle gains in bulk and turns laterad to pass beneath the supratemporal bar; as it does so its most anterior fibres have a nearly directly transverse direction, but with a slight caudad inclination from their origin. At this point there is a superficial division of the muscle, but the plane of separation does not extend deeply. In front of it the muscle arises from the intermuscular septum and dorsum and side of the skull as far forward as the middle of the orbit. The pars posterior has no attachment to the dorsum of the skull behind the supraorbital arch, but when freed from its origin lifts off the skull quite cleanly. When it is so detached and the free end carried forward and laterally, a deeper part of the muscle is found below it, and from which it separates quite cleanly for a little distance. These deeper fibres, however, merge with the deeper fibres of the pars anterior and the whole of the fibres converge to a short narrow tendon, which is inserted into the upper margin of the inner surface of the mandible a little way in front of the joint and deep to the insertion of the temporalis.

The M. Temporalis arises from the dorsum and anterior surface of the otic capsule and from the anterior surface of the parotic process and anterior edge of the quadrate, behind and lateral to the line of the supratemporal arch. The fibres pass laterad and ventrad to a relatively extensive insertion along the upper edge of the outer surface of the mandible for a short distance in front of the joint. Those fibres arising from the quadrate and parotic process close along side of it are partially separated from the rest in a manner suggestive of the massetericus minor of the frog.

The Relations of the Branches of the Vth Nerve.

The Foramen prooticum is placed below and to the inner side of the posterior root of the supratemporal arch.

The ramus mandibularis turns laterad and ventrad as soon as it separates from the other rami and passes down to enter the lower jaw just internal to the insertion of the temporalis. To reach this destination the muscle penetrates the M. temporalis, but does not divide it into superficial and deep portions. The Ramus maxillaris passes laterad and dorsad between the Mm. pterygoideus and temporalis. Lateral to the supratemporal arch, just at its posterior end, the nerve becomes superficial and runs ventrad and rostrad along the dividing plane between the muscles. Following the anterior margin of the temporalis when the other muscle passes back underneath it, the nerve next turns rostrad around the lower margin of the orbit.

The Ramus ophthalmicus profundus runs forward between the pterygoideus muscle and the side wall of the cranium.

THE MUSCLES OF THE HYOID SEGMENT.

The muscles of this segment present certain peculiarities which resemble the arrangement of these muscles in the Caecilians, and, being intermediate between the conditions there found and those of the Urodela, serve to assist in the comprehension of the caecilian muscles.

The Csv.2a presents two very definite portions which are here described as the partes superficialis and profunda.

Pars Superficialis.—This arises, under cover of the origin of the depressor mandibulae, from the inferior edge of the sulcus on the back of the parotic process and otic capsule. From this origin the fibres pass directly transversely and ventrally to an insertion into a mid-ventral raphe.

Pars Profunda.—This arises from the same edge below, i.e. lateral to, the superficial part of the muscle and from the tip of the cerato-hyal, which latter is placed immediately behind the upper end of the origin of the superficial part. At its origin this is a narrow thin ribbon and curves ventrad, laterad and rostrad deep to the posterior end of the mandible, passing first deep to the pars superficialis. Just medial to the mandible, a little way anterior to the joint, the fibres are gathered together to form a fine rounded cord and the muscle becomes bound to the lateral edge of the perimysium of the interhyoideus muscle which lies deep to it. The muscle fibres then diverge rather widely ; those most laterally placed run forward and mediad and reach almost to the symphysis, the median do not run forward so much. All the fibres are inserted into a median ventral raphe deep to the Csv.1.

The Csv.2b arises from the superficial fascia in the neighbourhood of the insertion of the depressor mandibulae. The fibres radiate widely. The anterior fibres have a direction nearly transverse but with an inclination caudad. The most posterior pass caudad with an inclination mediad. The former are inserted into a median raphe, the latter into the dense subcoracoid fascia, by which it is bound to the pectoral arch. The most posterior fibres are inserted well out from the mid-line, almost below the humero-scapular joint, and the line of insertion of the intermediate fibres curves from this point mediad and rostrad to the insertion of the anterior fibres.

The Depressor Mandibulae presents no indication of the pars notognathica. The muscle arises from the surface of the sulcus on the postero-dorsal area of the parotic process and the otic capsule. No trace of division into anterior and posterior parts can be found, and none of the fibres arise from the fascial structures behind the head. The fasciculi are gathered to a quite small area of insertion on the posterior end of the mandible, behind the joint.

The Interhyoideus is similar to that of *Amblystoma* but the anterior end of the ceratohyal is a good deal broader in this than in that genus, and in accord with this extra width of the available area insertion, the muscle is much more spread out anteriorly than in the other form, so much so that it appears to have an insertion into a mid-ventral raphe.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

The Constrictor Pharyngei arises from the dorsal fascia almost in common with the Dorso Laryngeus. The point of origin is immediately behind and above the postero-dorsal corner of the origin of the depressor mandibulae and under cover of the posterior continuation of the fascial covering of that muscle and the origin of the rhomboideus anterior muscle, but superficial to that of the M. cucullaris. The two muscles curve, alongside of each other, ventrad and caudad to be inserted at the mid-ventral line. The constrictor pharyngei is inserted into the medial raphe ventral to the larynx, the dorso-laryngeus curves dorsad to be inserted into the anterior end of the arytenoid cartilage at its dorsal edge.

The Hypobranchial Spinal Muscles.

The Genio-hyo-coracoideus arises, on each side of the symphysis, from the anterior end of the mandible. It is a narrow ribbon of fibres which extends straight back to be inserted on to the subcoracoid deep fascia, between the plane of insertion of the Csv.2b and the procoracoids. As the muscle passes the first arch of the hyoid it is bound thereto.

The Coraco-hyo-glossus arises as an anterior prolongation of the lateral portion of the rectus abdominis deep to the humero-scapular articulation. The more superficial fibres are inserted into the anterior arch of the hyoid alongside the hyoid plate. The deeper fibres are gathered to form a rounded muscle which passes forward above this arch and ends in a brush of fibres in the substance of the small tongue. The two portions of the muscle cannot be cleanly separated, except just as the glossal fibres dive above the cartilaginous arch.

The Capiti Pectoral Muscles.

The Cucullaris arises from the skull immediately behind, and deep to, the tip of the ceratohyal. It has the upper end of the origin of the pars superficialis of the Csv.2a superficial to it and the origin of the attrahens scapulae muscle deep to it. The fibres pass laterad and ventrad to be inserted into the anterior edge of the scapula just above the joint cavity.

The origin of the Attrahens Scapulae has just been mentioned; the fibres of the muscle radiate from the point-like origin to be inserted along the anterior margin of the scapula and suprascapula.

Spelerpes. (s. *Pseudotriton.*)

I have had for dissection one specimen of the adult, received from the American Museum of Natural History.

This genus reproduces, in the anatomy of its cephalic musculature, features already described in other genera. To describe these in detail would serve no good purpose; therefore, only those features of particular interest will be described.

No submentalis muscle was found.

The Csv.2b has a much more extensive origin than in any other form studied. The line of origin commences at the anterior margin of the well developed pars notognathica of the depressor mandibulae and extends back almost to the transverse level of the shoulder joint; this line, moreover, is placed higher than is the origin of the muscle in other forms—it is placed mid-way between the mid-lateral and mid-dorsal lines. The fibres of the muscle pass directly ventrad to be inserted into a mid-ventral raphe. The muscle extends so far back as to cover the procoracoids and the anterior part of the coracoids.

The tiny muscle which was described in *Amblystoma* under the name of Cerato-hyoideus Anterior is in this genus very well developed. It arises from the mandible close beside the symphysis and passes caudad and slightly laterad along the lateral margin of the ceratohyal cartilage till it lies beneath the posterior end of the mandible. It is inserted along the lateral edge of the ceratohyal.

This muscle is of interest because that in *Amblystoma* is so small that one questioned the wisdom of recognizing it as a separate muscle; this establishes its individuality.

The Laryngeal muscles are essentially similar to those of the Axolotl; this is of interest, as it is the perpetuation of a larval condition.

The muscles of mastication are more differentiated than those of any other Urodele studied. The Pterygoideus presents for description three parts.

The Pars Posterior arises as a fine point behind the posterior limit of the skull between the longissimus dorsi and the mid-dorsal intermuscular septum, and along the septum so far forward as to permit of the most anterior fibres passing laterad and ventrad with but a little inclination rostrad to the insertion. The lateral surface of the muscle is clothed by a strong fine tendinous perimysium into which the great majority of the fibres are inserted. This perimysium tapers and becomes thicker as it extends forward and finally, as a narrow tendon, is inserted into the apex of the coronoid process of the mandible.

The Pars Anterior arises from the dorsum of the skull in front of the last part. The muscle tapers to a short tendon which is inserted into the coronoid process just behind and medial to the other tendon. The most posterior fibres arise a little way posterior to the orbit, and these have a direction rostrad, laterad and ventrad. The most anterior fibres arise medial to the centre of the orbit and their direction to their insertion is caudad, laterad and ventrad.

The Pars Interna arises from the side wall of the skull beneath the pars anterior. There is a very definite cleavage plane between the two muscles and the fibres of the pars interna run caudad and laterad nearly horizontally, but with a slight inclination ventrad, converging to a short tendon by which they are inserted on to the upper edge of the inner surface of the mandible deep to all the other muscles of mastication just in front of the joint.

The Temporalis muscle arises from the anterodorsal surface of the otic capsule, parotic process and quadrate. Its fibres pass ventrad and slightly laterad to be inserted along a short length of the upper edge of the outer surface of the mandible behind the coronoid process.

The Quadrato-mandibularis is a small muscle which arises from the lower end of the quadrate and the skull under cover of the temporalis. Its fibres converge to be inserted into the upper edge of the inner surface of the mandible behind the tendons of the pterygoideus partes anterior and posterior. The general direction of the muscle is, from its insertion, laterad and rostrad and very slightly ventrad. This muscle passes dorsally to the tapered thin posterior end of the pars interna of the pterygoideus, the two crossing almost at right angles close to their insertions.

THE RELATIONS OF THE RAMI OF THE VTH NERVE.

The three rami of the nerve issue from the cranium under cover of the origin of the temporalis. The R. mandibularis turns at once laterad and ventrad between the temporalis and the quadrato-mandibularis; the main nerve plunges between Meckel's cartilage and the dentary, but just before so doing it gives off a branch which runs forward along the outer surface of the mandible. Where it enters the mandible the nerve lies between the temporal and quadrato-mandibularis insertions.

The Ramus Maxillaris passes forward against the wall of the skull till the anterior margin of the temporal muscle is reached; it at once turns laterad around the lower surface of the pars posterior of the pterygoid muscle, and then turns forward across the superficial face of that muscle.

The Ramus Ophthalmicus Profundus passes forward against the side wall of the cranium under cover of the origin of the pterygoideus muscle and the anterior portion of the origin of the quadrato-mandibularis.

2. Adult Anura.

The Frog. (Figs. 87–89.)

The following description of the muscles is based on a study of numerous specimens of *Hyla cerulea*, *H. aurea*, *Limnodynastes peronii* and *L. tasmaniensis*, and a single adult *Mixophyes fasciolatus*. The similarity of the muscles in all five forms was very close. Except in the depressor mandibulae of *Mixophyes*, no differences worthy of note were observed.

I have departed from the nomenclature of Gaupp's edition of Wiedersheim's "Anatomie des Froches", where it appeared desirable to reflect in the designations the homologies of the muscles with those of the fishes. This has only been done where it seemed reasonably certain that the homologies in question were correct.

The Submentalis, Csv.1a (Fig. 87).—This is a compact muscle whose fibres extend from one mandibular ramus to the other immediately behind the symphysis, without any tendinous intersection.

The Intermandibularis, Csv.1b.—This is the muscle which Gaupp terms the submaxillaris; it is, apparently beyond question, homologous with the intermandibularis of certain of the bony fishes and with the Csv.1b of the elasmobranchs. The simple Csv.1b of the younger tadpoles was found to give rise to a broad intermandibular sheet, in which a posterior portion, later developed, was differentiated from an anterior.

The Csv.1b¹ (Fig. 87) is the anterior portion of this sheet. The fibres arise from the inferior margin of the mandible, in its more transverse, anterior, part, on either side of the Csv.1a. They pass obliquely caudad and mediad and are inserted at the mid-line into a median raphe.

The Csv.1b² (Fig. 87) is the posterior portion. These fibres arise from the inner surface of the mandible close to the dorsal edge and pass towards the mid-line with a slight obliquity forwards, and are inserted into the median ventral tendinous intersection. The anterior limit of the origin of this portion is above the middle of the width of the last portion, the posterior limit is a little in front of the posterior end of the mandible. The greater part of the line of insertion lies deep to that of the last portion.

The Interhyoideus, Csv.2 (Fig. 87).—Gaupp designated this the "Subhyoideus". Its development indicates that it is homologous with the interhyoideus of the fishes.

This muscle arises from the upper, posterior, end of the anterior cornu of the hyoid (stylohyal) close to its attachment to the otocrane. Where this muscle arises, the portion of the stylohyal is situated dorsally and medially to the posterior end of the lower jaw, so high up and far toward the mid-line that the muscle appears to be coming from the postero-medial and dorsal area of the otocrane lateral to the origins of the levator scapulae superior and the rhomboideus anterior muscles. From this, comparatively narrow, origin the muscle widens out and becomes folded on itself. The anterior fibres cross the posterior intermandibular area behind the Csv.1b² to be inserted, in series with that muscle, into the mid-ventral raphe. The line of contact is very clearly marked by a transverse branch of the submaxillary artery, and the two muscles are quite freely separable. The anterior fibres, moreover, are not parallel with those of the mandibular sheet. There is a tolerable gap between the two muscles at the posterior margin of the Csv.1b² close to the mandible, through which the artery makes its way. The posterior margin of the gap is formed by the anterior fibres of Csv.2; these come into view from above and lateral to the posterior fibres of Csv.1b and, therefore, have a slight inclination caudad, as though coming from an origin on the mandible beneath the Csv.1b.

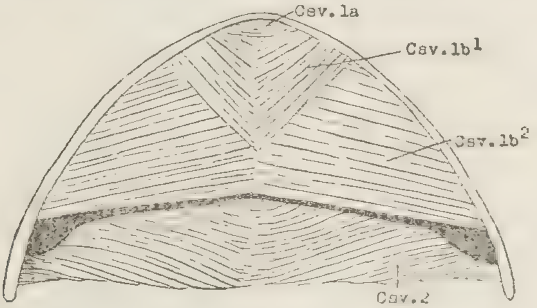


Fig. 87.—*Hyla*. The ventral constrictor muscles.

This definite break in the continuity between the mandibular and hyoid sheets is of interest. In a majority of the fishes and other amphibians which we have studied, these two ventral constrictor sheets become intimately blended along their contiguous margins. In those forms, however, the hyoid sheet is developed from a primitive superficial sheet and the interhyoideus lies dorsally to it. In the Frog there is, apparently, no primitive superficial hyoid sheet and the superficial constrictor of the adult is developed from the interhyoideus. This probably accounts for the definite break between the two, and the break provides evidence of the correctness of the interpretation here presented.

It has been stated above that the interhyoideus is folded on itself. Those fibres which arise from the highest point run obliquely forward toward the mid-line beneath those arising below and in front of them. They are not attached to the more superficial fibres. When the head is strongly dorsi-flexed the muscle becomes unfolded, and the posterior fibres are exposed. The posterior limit of the muscle can now be observed to extend from their origin to the mid-ventral line, passing dorsally to the posterior end of the mandible and slightly in front of it on each side.

This line corresponds very closely with the line of fusion of the posterior margins of the opercular folds to the ventrum of the throat at the metamorphosis of the Axolotl to the adult *Amblystoma*. In both the *Amblystoma* and the Frog there is a narrow membranous sheet connecting the perimysium and the skin along the posterior margin of the superficial hyoid constrictor. In the former it marks the line of closure of the branchial chamber. It may be designated the " post-opercular myo-integumental fascia ".

When the head of the frog is slightly ventri-flexed, the fold of the Csv.2 passes behind this fascia and the anterior margin of the muscle comes to lie almost directly beneath it.

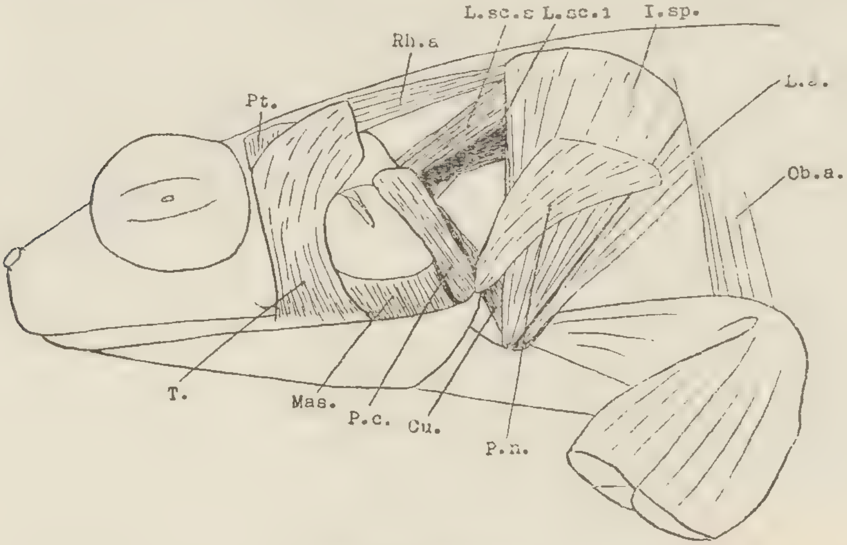


Fig. 88.—*Mixophyes.*

Innervation.—The break between the mandibular and hyoid ventral constrictor sheets enables one to state with the utmost confidence that the former is innervated by the Vth nerve alone, and that this nerve does not send any twigs backward across the interval. The communication between the VIIth and IXth nerves debars one from speaking with equal certainty about the innervation of any of the muscles innervated from the hyoid trunk of the VIIth. One can, however, assert with confidence that the Csv.2 is innervated only by twigs which are all traceable to the ramus jugularis of the hyomandibular trunk of VII.

The Depressor Mandibulae.

The Pars Cephalognathica (Fig. 88, P.c.) arises from the postero-lateral and superior corner of the auditory capsule immediately above the centre of the tympanic annulus, and from the superficial perimysium of the pars lateralis of the temporalis muscle dorsally and medially to that point. From this origin the fibres pass ventrad, laterad and caudad, to be inserted on to the outer side of the mandible immediately behind the joint.

The Pars Notognathica (Fig. 88, P.n.) arises from the fascia dorsalis superficially to the suprascapula and the infraspinatus muscle, this origin extending from the anterior margin of the suprascapula back as far as the anterior margin of the superficial oblique abdominal muscle. By the fascia dorsalis the origin of the muscle is carried to the mid-dorsal line, but the dorsal margin of the muscle itself is nearly coincident with that of the suprascapula beneath it, except posteriorly, where it falls to a lower level between the fascia of origin of the abdominal muscle superficial to it and the latissimus dorsi muscle deep to it. From this wide origin the fibres converge to be inserted on to the posterior end of the mandible, behind the pars cephalognathica. A broad ribbon at its origin, this muscle becomes a narrow, and thicker, muscle at tis insertion.

Innervation.—Both parts of the depressor mandibulae are innervated by twigs from the ramus jugularis of the hyoid trunk of the VIIth nerve.

Edgeworth (1911, p. 217) states that in " Rana, at metamorphosis, the orbito-hyoideus extends upwards on the atrophy of the processus muscularis of the palato-quadrate, the lower end of the orbito-hyoideus gains a new insertion to the hind end of the lower jaw. The cerato-hyo-angularis, suspensorio-angularis and quadrato-angularis assume a more vertical position on rotation of the palato-quadrate, and form the inner portion, whilst the original orbitohyoideus forms the outer portion, of the depressor mandibulae ".

Edgeworth, apparently, bases the whole of his descriptions on the study of serial sections. I have found that such study, even when carried out on sections cut in all three planes, is liable to be most misleading. The closest study fails altogether, at times, to discover the cleavage planes between muscles whose component fibres are parallel or only slightly inclined to one another. It is, therefore, more than probable that the development of this muscle in *Rana* is similar to that in the frogs I have studied.

Edgeworth adopts the nomenclature of Schultze.

The synonymy is as follows :

Edgeworth-Schultze.	This work.
Orbito-hyoideus	Dilator hyoidei
Cerato-hyo-angularis	Pars notognathica
Suspensorio-angularis	Pars cephalognathica
Quadrato-angularis	Massetericus minimus

When it is remembered that the pars cephalognathica extends upward and backward across the surface of the processus muscularis under the dilator hyoidei and, in later stages, nearly parallel with it, it is readily understandable that the increasing bulk of this muscle should have been mistaken, in serial sections, for the other in a new situation and with new attachments. This description of the development of the depressor mandibulae by Edgeworth caused me to review again, and with added care, my own dissections. I am quite confident that the pars cephalognathica of the early tadpole gives rise to the main part of the same muscle in the adult. That some few fibres of the caducous dilator hyoidei may persist and contribute to the adult muscle is not impossible, but I can find no evidence of this.

If I have not correctly identified the quadrato-angularis, then the muscle is not present in any stage of the development of the several frogs I have studied. The error of regarding this as one of the components of the depressor series probably comes from the fact that it arises very low down on the quadrate and is inserted directly above the joint on to the superior edge of the mandible. When first found in my tadpoles it had a more vertical direction than it has in the adult.

The Muscles of Mastication.

The six muscles which were found in the later tadpoles are all recognizable in the adult.

The Pterygoideus (Fig. 88, P.t.) arises from the dorsum and side wall of the skull behind the orbit and in front of the temporalis muscle, it is for the most part covered by the latter muscle, but appears superficially between it and the orbit close to the mid-line dorsally. From its origin the muscle tapers rapidly as it passes ventrad, laterad and slightly caudad, beneath the temporalis and terminates in a fine ribbon-like tendon which continues the direction of the muscle as it lies against the lower edge of the anterior wall of the auditory capsule. It passes across the dorsal surface of the os transversum, pterygoid bone of authors, in contact with the anterior surface of the quadrate, and is inserted near the inferior margin, on the inner side of the mandible just in front of the joint.

The Temporalis muscle (Fig. 88, T.) must be described in two parts. The Pars lateralis is the depressor labii superioris longus of the early tadpoles, and it constitutes a superficial and lateral portion of the muscle. It arises from the whole of the dorsum of the otocrane, extending medially over the top of the curve and down a short distance on the posterior slope. From this origin the muscle passes cephalad, ventrad and laterad. Its outer margin lies in contact with the inner surface of the post-orbital descending limb of the squamosal and the quadrato-jugal. Its insertion is a fleshy one on to the outer and upper surface of the mandible in front of the tympanic annulus.

The Pars medialis is the temporalis of the tadpoles, the two portions are very easily separated and leave perfectly smooth surfaces after separation. The origin is from the antero-superior medial corner of the otocrane and from the dorsum of the skull medial thereto, between the last muscle behind and laterally and the pterygoideus in front and medially. It is a slightly smaller muscle than the other division of the temporalis ; its direction is parallel to the other. The insertion is, by a short ribbon of tendon, into the mandible medial to the lateral division.

The Masseter Major (Fig. 88, Mas.).—This is the masseter of the tadpoles. It arises from the inferior edge of the post-orbital bar and from the tympanic annulus. The muscle is a quite thin sheet of short fibres which descend almost vertically to be inserted on to the upper edge and outer surface of the mandible behind the temporalis. The anterior portion of the muscle, arising from the squamosal, is the thicker and there is here some convergence of the fibres into an arcuate insertion into the upper surface of the mandible immediately behind that of the temporalis. Behind this the muscle is thinner and the insertion is carried, by a short fascial sheet, down the outer surface of the mandible almost to the inferior margin.

The Masseter Minor, the quadrato-mandibularis of the tadpoles.—This is a short triangular muscle which arises from the edge of the quadrate below the quadrato-jugal and is inserted into the inner edge of the upper surface of the mandible. The most anterior fibres of this muscle pass ventrad nearly vertically, with a slight inclination cephalad. The posterior fibres pass cephalad with a slight inclination ventrad.

The Masseter Minima.—This muscle has not, so far as I am aware, been previously described in the adult frog; it is apparently the quadrato-angularis of Schultze's description of tadpoles. It is a small flattened narrow muscle, pointed at both ends, which arises from the tip of the quadrate and inner surface of the extreme posterior end of the quadrato-jugal and passes forward along the upper surface of the posterior end of the mandible, between the masseter muscles, to an insertion immediately behind that of the masseter major, on to the upper surface of the mandible.

Innervation.—All these six muscles of mastication are innervated by twigs which they receive from the ramus mandibularis V as that nerve passes among them on its way to the ventrum of the mouth.

The course of the ramus mandibularis V is as follows. When it leaves the common trunk it passes dorsad, laterad and cephalad between the temporalis on its outer side and the pterygoideus medial to it, and comes into view as a subcutaneous structure between these muscles some little distance behind the orbit. It turns more directly laterad and may cross the temporalis and pass out of sight again at its lateral margin by running beneath the descending limb of the squamosal, or it may reach the same position beneath this bone more directly by penetrating the pars lateralis of the temporal muscle. Beneath the squamosal it turns caudad and perforates the masseter major, and continues for a short distance between this muscle and the masseter minima. It next turns cephalad again, passes over the last muscle and turns ventrad external to the ramus of the mandible and the masseter minor. Finally it perforates the posterior fascial insertion of the masseter major and turns mediad and cephalad to reach the ventrum of the mouth.

Deep Constrictors, apparently Innervated only by the IXth and Xth Nerves.

The Constrictor pharyngei (Petro-hyoideus anterior, of Gaupp) (Fig. 89, C.ph.) arises on each side from the stylohyal cartilage high up behind the origin of the Csv.2, and from the otocrane above and medial to this. From this restricted area of origin the muscle courses round on the under side of the pharynx, beneath the pharyngeal mucosa. The muscle widens considerably as it passes toward the mid-ventral line, and is inserted on to the lateral edge of the hyoid plate, from the root of the posterior cornu forward to that of the anterior cornu.

The three muscles which Gaupp designated posterior petro-hyoid are, probably, together homologous with the dorso-laryngeal and last interbranchial of the Axolotl and perennibranchiate urodeles generally. It will be remembered that in the tadpole with the fully developed branchial arches there is but a single muscle and that all three of the muscles we have to describe here are developed later than that one.

The three muscles arise together from the back of the skull between the temporalis above, the otoscapularis laterally, and the rhomboideus anterior medially, but slightly ventral to all three. From this origin they pass caudad, mediad and ventrad, superficial to the cucullaris and levator scapulae inferior, but deep to the levator scapulae superior. For purposes of description I have designated two of them cranio-hyoideus and cranio-laryngeus respectively; the third is the dorso-laryngeus.

The Cranio-hyoideus (Fig. 89, C.h.a.), having reached the ventrum of the pharynx, turns more directly transversely than the cranio-laryngeus behind it, leaving a triangular gap between their ventral ends. Nearly, but not quite, parallel to the hinder margin of the constrictor pharyngei, and a little way behind it, this muscle passes to the body of the hyoid just behind its middle cornu, and is inserted thereon.

The Cranio-hyoideus (Fig. 89, Cr.hy.) is inserted to the outer edge of the posterior cornu of the hyoid (the thyreohyoid) dorsally to the insertion of the hyoglossus, and near the posterior end of the cornu a little distance caudad to the point where the last muscle gains the dorsal surface of the body.

The Dorso-laryngeus (Fig. 89, D.l.) may, perhaps, be the homologue of the dorso-laryngis of Drüner's description of the Urodela ; if so, the other two muscles will be regarded as added muscles differentiated from the single primordium present in the tadpole. It lies almost in contact with the posterior margin of the last muscle, but is continued past the insertion of the other and is inserted on to the lateral cartilage of the larynx immediately posterior to the point where that is bound to the end of the posterior hyoid cornu.

Innervation.—It has been quite impossible to satisfy myself that I have successfully separated the components of the nerve tangle. I therefore content myself with the statement that I have found none other than branches from these nerves reaching any one of these four muscles. I believe that the constrictor pharyngei is innervated by the IXth and the others by the Xth nerve, but I cannot be certain. The question must be decided by the study of appropriately stained serial sections, or by stimulation of the nerves.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The Genio-hyoideus presents three very definitely defined portions. Gaupp illustrates these three portions, but fails to describe them separately.

The Genio-hyoideus pars lateralis (Fig. 89, G.h.l.) is a narrow ribbon which arises from the inner surface of the mandible towards its dorsal edge just lateral to the origin of the submentalis ; it passes thence directly caudad to be inserted on to the outer edge of the middle cornu of the hyoid. As it passes back it lies beneath the loop of the stylohyal. A large branch of the hypoglossal (1st spinal) nerve passes forward along its dorsal surface. At its insertion it has the dorsally folded lateral margin of the sterno-hyoideus medial to it.

The Genio-hyoideus pars intermedius (Fig. 89, G.h.i.) is a similar ribbon-like muscle which arises just medial to the last, but closer to the lower edge of the mandible under cover of the

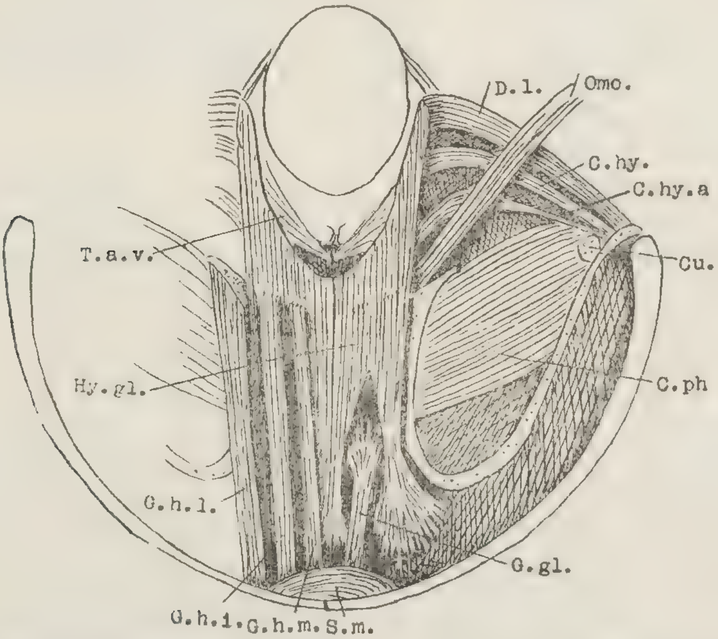


Fig. 89.—*Hyla*. Muscles of the ventrum of the head. C.hy., M. craniohyoideus ; C.hy.a., M. craniohyoideus anterior ; S.m., M. submentalis ; G.h.m., M. geniohyoideus medialis ; G.h.i., M. geniohyoideus intermedius ; G.h.l., M. geniohyoideus lateralis ; T.a.v., M. thyroarytenoideus ventralis.

submentalis. It passes caudad to be inserted on to the perimysium of the hyoglossal muscle, a small median bundle of fasciculi gaining an insertion on to the posterior margin of the hyoid.

The Genio-hyoideus pars medialis (Fig. 89, G.h.m.) is a third narrow ribbon which arises from the upper, inner edge of the mandible right alongside of the symphysis, separated from the origin of the pars intermedius by the origin of the genio-glossus. It passes back to be inserted in like manner to the last part, but superficial to it. By the perimysium of the hyo-glossus muscle, the insertion of these last two is carried back to the antero-lateral margin of the larynx.

The Genio-glossus muscle (Fig. 89, G.gl.) arises from the inner surface of the mandible between two genio-hyo-laryngeal muscles. It is a relatively short and stout muscle which passes caudad, dorsad and slightly mediad, to terminate in a brush of fibres which extend through the connective tissues of the tongue for two-thirds of its length from the anterior tip.

The Hyo-glossus (Fig. 89, Hy.gl.) is a surprisingly massive muscle which arises from the posterior cornu of the hyoid throughout its length and passes forward ventrally to the body of the hyoid, and then turns dorsad and breaks up into brushes of fasciculi. Three main divisions of these may be recognized, a median and two lateral. The median fasciculi are inserted in the tough submucous tissue along the mid-line of the tongue from close to the base, right forward almost to the tip, with those of the genio-glossus on either side. The fasciculi of the two lateral groups end in the same tissue along the margin and lateral area of the tongue outside the genio-glossus.

Since the antero-lateral corner of the larynx is bound to the posterior hyoid cornu, this muscle, when antagonized by the genio-glossus and genio-hyoideus, is capable of pulling the larynx forward and assisting in dilating it.

Innervation.—These muscles are innervated by the hypoglossal nerve. Whether the spinal II components of the trunk of this nerve reach these muscles or not, is impossible of determination by dissection.

THE CAPITI-PECTORAL MUSCLES.

Including the Omo-hyoideus, there are five of these to be described.

The Rhomboideus Anterior (Fig. 88, Rh.a.) arises from the posterior margin of the skull superficially, on either side of the mid-line and medial to the auditory capsule. The fibres pass directly backward to be inserted into the dorsal margin of the suprascapula. The longest fibres are medial, and are inserted farthest back along the dorsal edge of the suprascapula.

This muscle appears quite early in the development as a delamination of the first dorsal myomere which later grows backwards and gains an insertion on to the suprascapula.

Innervation.—The muscle is innervated by a twig which it was found impossible to trace back through the dorsal trunk muscle, from which it emerged beneath the muscle. It is probable that the twig came from the second spinal nerve, as in *Rana*.

The Levator Scapulae Superior (Fig. 88, L.sc.s.) arises from the back of the skull medial to the auditory capsule, ventrally to and behind the posterior limit of the origin of the temporalis. At its origin the muscle is fleshy and nearly cylindrical in section. From its origin it extends caudad, mediad and dorsad, and is inserted on to the anterior margin of the scapula just below the suprascapula. At its insertion the fibres are somewhat spread out, so that the muscle is here flattened.

Innervation.—This muscle is innervated by the second spinal nerve. The motor branch to this nerve leaves the main nerve before it combines with the first to form the ventral spinalis (Hypoglossal) trunk to the hypobranchial spinal muscles.

The Cucullaris (Fig. 88, Cu.) is the Trapezius of Edgeworth (1911) and the Capiti-scapularis of Furbringer (1875). The muscle arises from the postero-superior margin of the auditory capsule beneath the origin of the pars cephalognathica of the depressor mandibulae, behind the temporalis and lateral and slightly dorsal to the levator scapulae superior. It passes from its origin ventrad, laterad and caudad, to be inserted on to the scapula just above and lateral to the glenoid cavity.

Innervation.—This is by a twig which was traced back to the main trunk of the Xth nerve, distal to the point where the communications with the IXth nerve are effected.

The Levator Scapulae Inferior (Fig. 88, L.sc.i.) arises from the back of the skull beneath the superficial levator of the scapula. It extends backwards and slightly laterally to be inserted on to the deep surface of the scapula underneath the insertion of the same muscle, extending backwards across the deep surface of the scapula for a little distance.

The Omohyoideus (Fig. 89, Omo.) is included here because of its origin, at least in part, from a cephalic muscle, and because it is one of the muscles innervated by the hypoglossal nerve, formed by spinal nerves I and II.

It arises from the ventral surface of the body of the hyoid, medially to the middle cornu, and passes caudad, laterad and slightly dorsad. It crosses the dorsal surface of the scapula diagonally, above the glenoid cavity. At the posterior edge of the bone it curls round its posterior surface and becomes inserted, under the tendons of the infraspinatus and latissimus dorsi, on to the posterior surface of the scapula.

Innervation.—This is, as already stated, by the hypoglossal nerve.

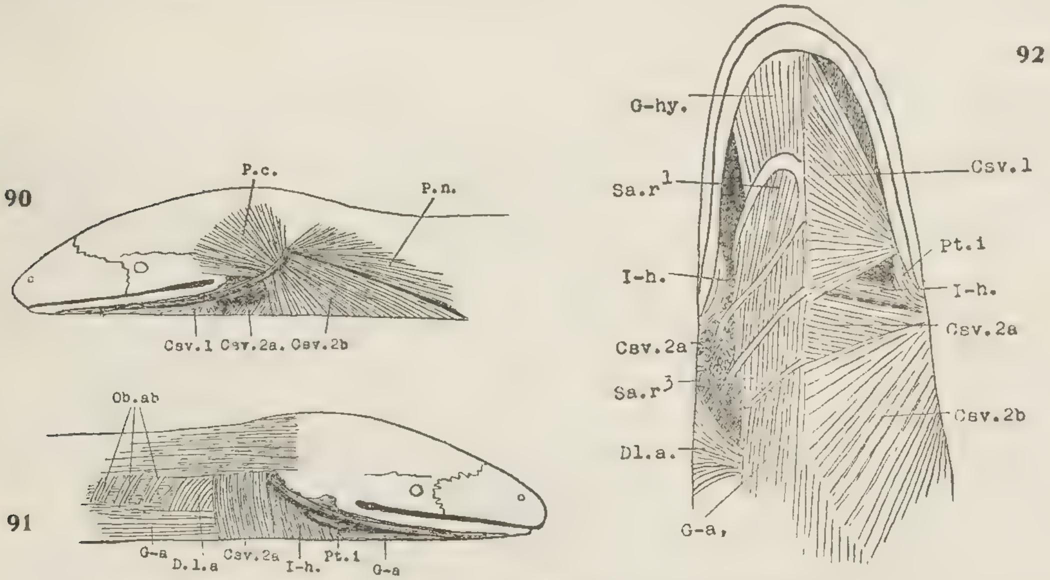
3. Adult Caecilians.

The Cephalic Muscles of Ichthyophis glutinosa.

(Figs. 90–92.)

Material.—This consisted of two very well preserved specimens of *I. glutinosa* which I received from Dr. J. Pearson, now Director of the Tasmanian Museum; and a collection of sets of serial sections of several of the Caecilians from Prof. H. W. Norris, of Grinnel. I wish to tender my grateful thanks to these gentlemen for this assistance.

The serial sections originally formed part of the material on which the work of Norris and Hughes was based when they wrote their account of the Cranial and Anterior Spinal Nerves of the Caecilian Amphibians. Prepared and stained primarily for the study of the nerves, they were counterstained with a carmine preparation and are beautiful slides for general study.



Figs. 90-92.—*Ichthyophis.* G.a., M. genio-abdominis; Pt.i., M. pterygoideus internus.

It may be of interest to record that, notwithstanding the perfection of these slides, it was not found possible to determine the details of the cephalic musculature by the study of them alone. I had the slides in my possession long before I received the complete specimen, and had, as I thought, made a complete description of the muscles. On receipt of the complete specimen, dissection was undertaken with a view to seeing the muscles actually in their relation one to another, and not with the intention of checking the description already prepared. It was with no little surprise that these relations were found to be different from those visualized from the sections. In several instances the boundaries of juxtaposed muscles had been wrongly located. This was in those instances where the direction of the fibres was nearly parallel.

A return to the sections, after the dissection, fully confirmed the later findings.

I may remark that, in the course of the study of the muscles in the serial sections, I very naturally also studied their innervation, and, as was to be expected, found it always to be as described by Norris and Hughes. Particularly have I studied the remarkable Csv.2b in this connection and find that there is certainly only the one motor supply to this muscle, namely, that described by Norris and Hughes from the ramus jugularis of the hyomandibular division of the VIIth nerve.

THE MUSCLES OF THE MANDIBULAR SEGMENT.*

Unfortunately I have not been able to consult the work on *Ichthyophis* by the brothers Sarasin. I give below the synonymy of the muscles from Wiedersheim (1879) and Norris and Hughes. These latter authors, for the most part, contented themselves with referring to the muscles in the course of their description of the nerves. I have been able to determine their synonymy with some certainty by actually identifying the muscles in the slides by comparison of their illustrations with the sections they illustrated.

Wiedersheim.	Norris and Hughes.	This work.
	Masseter	Masseter
Masseter	Temporalis	Pterygoideus
	Petrygoideus	Pterygoideus internus
Not described	Levator quadrati	Levator quadrati
Intermandibularis (anterior part only)	Intermandibularis	Intermandibularis

The Intermandibularis (Figs. 90, 91, Csv.1) muscle alone represents the superficial constrictor sheet of the mandibular segment, there being no submentalis. Each muscle is a triangular sheet which arises from the inner surface of the mandible well back towards the joint. The fibres diverge widely as they pass towards the mid-line to be inserted into the median raphe. The most anterior pass almost directly rostrad, reaching nearly to the symphysis, the posterior fibres nearly transversely but with an inclination caudad.

The Pterygoideus muscle arises from the lateral wall of the cranium and from its roof under cover of the temporal roofing bones. The anterior limit of the origin is placed medial to the orbit, the posterior lies to the inner side of the auditory capsule. It appears that none of the fibres arise from the deep surface of the temporal roof, but that the dorsal limit of the origin is the line along which the temporal squame of the parietal meets the descending limb of the bone. The inferior line of the origin of the muscle is but a little below this. The insertion is by short tendon, to which all the fibres converge, into the inner surface of the mandible towards its upper edge in front of the joint.

The Masseter arises from the ventral surface of the temporal roof and from the medial surface of the lateral ascending process of the quadrate. From this origin the fibres pass to be inserted into the upper edge of the mandible behind and slightly external to the insertion of the pterygoideus.

The Levator Quadrati lies deep to both of these muscles ; it is a narrow strip of short fibres which arise from the alisphenoid region of the side wall of the cranium beneath the origin of the pterygoideus anteriorly, and medial to the masseter posteriorly. The fibres pass ventrad and very slightly laterad to be inserted into the anterior process of the quadrate.

The Pterygoideus Internus (Fig. 92, Pt.i.) arises from the postero-median edge of the os transversum (pterygoid bone, of Wiedersheim and Sarasins). The area of origin is quite small, but the muscle expands very rapidly as it passes caudad and laterad, so that it is a relatively bulky muscle as it lies beneath the mandible at its insertion, on to the inferior surface thereof, below the joint.

THE RELATIONS OF THE RAMI OF THE VTH NERVE.

The Gasserian ganglion lies in a fossa above the posterior end of the origin of the levator quadrati, and the ramus mandibularis passes ventrad to the foramen in the gonial by which it gains the canal in the mandible so directly that one may trace the whole of this course of the nerve in one single transverse section 30μ thick. As it enters the gonial it has the insertion of the pterygoideus in front of it and to the inner side, and that of the masseter behind and external to it. As it passes down from the ganglion the posterior end of the pterygoid muscle lies deep to it and the masseter superficial to it.

---

* Nothing is known of the development of any of the muscles of the Caecilians ; their segmental origin is therefore assumed from their innervation.

The Ramus ophthalmicus profundus and the ramus maxillaris run directly forward between the origin of the levator quadrati below them and that of the masseter above. The former maintains this position close against the cranial wall all the way to the orbit, the latter soon becomes separated from the former by passing superficially to the pterygoid. It continues forward between the pterygoid and the masseter to the anterior boundary of the muscles.

THE MUSCLES OF THE HYOID SEGMENT.

The synonymy is as follows :

Wiedersheim.	Norris and Hughes.	This work.
Intermaxillaris posterior part	Interhyoideus (of the urodeles)	Interhyoideus and Csv.2a.
Omo-humero-maxillaris	Omo-humero-maxillaris	Csv.2b
Cephalo-dorso-maxillaris	Depressor mandibulae	Depressor mandibulae
	Levator hyoidei	Not found
	Cerato-hyoideus-externus	,, ,,

The Ventral Constrictor sheet innervated by the VIIth nerve presents three divisions.

The Interhyoideus (Fig. 92, I-h.) is a relatively narrow band of fibres which arise high up along the ceratohyal, deeply placed beneath the post-articular projection of the mandible and its muscles, the pterygoideus internus and the Csv.2b. From that origin they pass ventrad, mediad and rostrad, to be inserted into the mid-ventral raphe deep to the posterior portion of the Csv.1b (the intermandibularis).

The Csv.2a (Fig. 92) is a broader sheet of fibres which arise from a fascia which covers the trunk muscles behind the origin of the interhyoideus. These Csv.2a fibres arise further dorsally than the interhyoideus fibres. At their origin they lie deep to the anterior end of the thyroid gland. For the greater part of their length the 2a fibres are hidden beneath the Csv.2b ; they pass mediad, parallel to the interhyoideus fibres to be inserted into the mid-ventral raphe behind them.

The Csv.2b (Fig. 92) arise from the outer edge and postero-ventral surface of the post-articular portion of the lower jaw. From this origin the fasciculi radiate widely. The most anterior have a direction mediad and ventrad with a slight inclination rostrad. The most posterior, those arising from near the tip of the gonial, have a direction almost directly caudad, with a slight inclination ventrad. These latter are inserted into the fascia dorsalis just below the mid-lateral line as far behind their origin as half the length of the head ; the anterior fibres are inserted into the abdominal fascia at the mid-ventral line superficially to the Csv.2a fibres. The intermediate fibres are inserted along a curved line joining these two extremes.

The Depressor mandibulae presents two clearly defined parts.

The Pars Cephalognathica (Fig. 90, P.c.) has an extensive origin from the dorsal surfaces of the squamosal and parietal bones. The insertion is into the anterior edge and surface of the post-articular portion of the gonial. The foremost fibres pass directly caudad from origin to insertion just above the joint, the most posterior pass ventrad and rostrad to their insertion at the top of the anterior edge of the gonial.

The Pars Notognathica (Fig. 90, P.n.) is a somewhat larger muscle than the last. It arises from the fascia dorsalis above the Csv.2b. In outline the muscle is triangular, the apex being at the insertion into the tip of the gonial. The inferior fibres of the muscle are the longest ; these run parallel with the dorsal fibres of the Csv.2b. The most anterior fibres arise almost at the mid-dorsal line and pass rostrad and ventrad to their insertion.

I have been unable to find a levator hyoidei in any of the caecilians which I have been able to study. Norris and Hughes illustrate a levator hyoidei in a late larval stage of *Ichthyophis.* Unfortunately I have not been able to study any larval stages of these amphibians. Apparently the levator hyoidei of the larva is either a caducous muscle or it becomes converted into the pars notognathica of the adult. I have been unable to find any other muscles than those just described, which are innervated by the VIIth nerve. The illustration given by Norris and Hughes (1920) leads me to believe that it is portion of the pterygoideus internus which they have so identified. This, of course, is innervated by the Vth nerve.

Discussion.—The same muscles that were found in the Urodela are present in the Caecilia in the hyoid segment, though not arranged in quite the same manner.

The situation of the interhyoideus and its insertion into the mid-ventral raphe is a more primitive arrangement than has been met in any other amphibian, and is, indeed, a return to the elasmobranchian condition.

The origin of the Csv.2a is rather more deeply placed than we have found it in other amphibians, but not sufficiently so to raise any doubt as to its correct identification. It will be remembered that in the urodeles this origin is carried deeply by the attachment of the stylohyal to the back of the cranium. In the caecilians there has been a remarkable elongation of the neck region, and one of the results (or causes) of this has been that continued backward trend of the dorsal ends of the branchial cartilages which we find correlated with the more posterior situation of the origin of the Csv.2a. One remarks that, in the urodeles the thyroid gland is placed just behind and superficially to the origin of the Csv.2a, as it is in the caecilians.

The innervation and the origin of the Csv.2b are the two features of this muscle in the caecilians which lead us directly to its identification. Here, as in other amphibians, the muscle arises from a superficial fascia by which it is bound to the posterior end of the superficial surface of the mandible immediately below the pars notognathica of the depressor mandibulae. Its wide insertion and long posterior extension must be regarded as resultants of the elongation of the neck region.

Although I have identified one of the muscles of *Ichthyophis* as the interhyoideus, attention should, perhaps, be drawn to the fact that this is not the muscle which Norris and Hughes identify as the cerato-hyoideus externus. This muscle they illustrate in a section of a larval *Ichthyophis*. That which they identify thus is placed more superficially than is the interhyoideus of my description. It is, of course, possible that the muscle may have been more superficially placed in the larva.

MUSCLES OF THE BRANCHIAL SEGMENTS.

The Subarcualis Rectus I (Fig. 92, Sa.r^1) (Cerato-hyoideus internus of Norris and Hughes).—This is a short muscle which arises, dorsally to the genio-abdominis, from the posterior edge of the ceratohyal cartilage for the greater part of its length. The fibres pass caudad and laterad to be inserted into the anterior edge of the first ceratobranchial cartilage. This muscle extends further out, laterally, than do the other straight subarcual muscles, and, moreover, its fibres have a definite obliquity.

Subarcuales Recti II and III (Fig. 92, Sa.r.2 and 3) are two short muscles placed between the first and second, and second and third ceratobranchial cartilages above the genio-abdominis; they are inseparable from, and their fibres run absolutely parallel with, those of the larger muscle. The muscles were not noted by Norris and Hughes.

Subarcualis Rectus IV.—Behind the third ceratobranchial cartilage there is a thin layer of short longitudinal fibres which arise from the posterior edge of the inferior surface of the cartilage just as do the fibres of recti II and III from the other cartilages. These fibres are inserted irregularly into the rather dense connective tissue which lies between and below the laryngeal muscles. The commingling of these fibres and those of certain of the laryngeal muscles was remarked on by Norris and Hughes.

Innervation.—This is by a branch which continues forward that ramulus of the laryngeus recurrens which innervates the constrictor pharyngei.

The Constrictor Pharyngei (Hyopharyngeus internus of Norris and Hughes) is doubtless the homologue of the transversus ventralis 4 which gives rise to the constrictor pharyngei in the urodeles. It arises from the posterior margin of the greater part of the length of the third (the last) branchial arch on each side and its fibres pass directly mediad to be inserted into a mid-ventral raphe and, in part, into the trachea.

The Dorso-laryngeus is apparently represented by two portions.

The Pars Dorsalis (Figs. 91, 92, D.l.d.) (Levator Arcuum Branchialium of Norris and Hughes) arises from the fascia investing the trunk muscles deep to the inferior margin of the pars notognathica of the depressor mandibulae and the posterior origin of the Csv.2b. From this origin the fibres pass ventrad and caudad, converging to be inserted into a tendinous condensation of tissues by which it is bound to the extreme tips of the second and third branchial arches.

Pars Ventralis (Hyo-pharyngeus of Norris and Hughes) arises from the inferior surface of the posterior edge of the fourth arch, third branchial, and its fibres pass mediad and caudad to meet the other muscle in the mid-line dorsal to the larynx. The muscle is incompletely divided into a more median and a lateral portion at its origin.

Norris and Hughes also describe a Dilator laryngis, a Sphincter laryngis and a Laryngeus ventralis.

There is a little doubt as to whether I have identified the Dilator correctly. I find a very definite and quite separated bundle of fibres arising from the third branchial cartilage out near the most lateral limit of the pars ventralis of the dorso-laryngeus and passing across ventrally to the other muscles, and obliquely to their fibres, to an insertion into the arytenoid cartilage. Norris and Hughes depict the dilator between the constrictor pharyngei and the pars ventralis of the dorso-laryngeus.

The Sphincter forms an almost complete collar for the entrance to the larynx. Its fibres are inserted into a mid-dorsal raphe. Its weakest point is ventrally, where it is apparently fused with the tiny Laryngeus ventralis of the larva.

In addition to these, I find a muscle which appears to be the Interbranchialis 4 which these authors describe in *Herpele*. It is a narrow thin muscle which arises from the tip of the last two branchial arches by a fine tendon and, widening slightly as it passes caudad and mediad, is inserted a little distance behind the larynx into the tissue at the side of the trachea. The muscle is certainly not a fourth interbranchial; it may perhaps be derived from a fifth arch, or it may be an anterior slip of the rectus abdominis.

The Hypobranchial Spinal Muscles.

The Genio-abdominis (Figs. 91, 92, G-d.) (Thoracicohyoideus of Wiedersheim and of Norris and Hughes) arises from the mandible just to one side of the symphysis. The fibres pass back to be inserted on to the anterior edge of the first ceratobranchial cartilage. From the posterior edge of this cartilage the muscle takes a second origin and continues caudad to an intersection placed below, and attached to, the third ceratobranchial. Behind this intersection the muscle is continued to become fused with the rectus abdominis.

The dorsal surface of the muscle is practically continuous with the interarcual muscles between the branchial cartilages.

The Genio-hyoideus (Fig. 92, G-hy.) muscle arises from the mandible dorsal to the genio-abdominis and, being wider than this last, may be seen lateral to it, before the more superficial muscle is removed. It is inserted into the anterior edge of the ceratohyal cartilage and to the central piece which connects this to its fellow.

4. Review.

The several short discussions which have been introduced in the course of the description of the cephalic musculature of the abranchiate amphibians renders a lengthy review of their features unnecessary.

The Pterygoideus Muscle.

A final review of the evidence on which this muscle was identified as the pterygoideus in the Elasmobranch fishes is advisable before passing to the higher vertebrata.

The most recent discussion on the origin of the pterygoideus muscle with which I am acquainted is that in Dr. Lightoller's work on "Probable Homologues in other Vertebrates of some of the Elasmobranch Constrictors and Levators".

I am deeply indebted to Dr. Lightoller, not merely for permission to read his typescript, but for the present of a copy of it, together with a set of his illustrations. I found his work exceedingly valuable, and I owe not a little to his stimulating criticisms of my own work as it progressed.

He and I have approached the same problems from rather different angles, and, after numerous discussions, have agreed to differ on certain questions. One of these is the origin (evolution) of the pterygoideus. That we should be unable to see eye to eye on this question may be regarded as one of those numerous instances which illustrates the importance of the personal factor in equations of this kind.

Now it is unquestionable that the levator maxillae superior of *Carcharinus* is very similar to the pterygoideus of the amphibians, but it is believed that this similarity is more apparent than real. This muscle is situated behind and lateral to the mandibular and maxillary rami of the fifth nerve, whilst the pterygoid of the amphibians is situated medial to and in front of these nerves.

It may also be pointed out that the levator maxillae superior could, apparently, only attain to its insertion on the lower jaw by means of the subdermal fascial layers, so that a mandibular adductor derived from this muscle should have its insertion superficial to that of the muscles derived from the elasmobranch adductors, whereas the insertion of the pterygoideus in the tetrapods is always deep to the other muscles of mastication.

Another line of comparison offers further support for the interpretation of the origin of the pterygoideus muscle which is here advanced.

In such bony fishes as *Amia*, *Polypterus*, *Girella* and *Platycephalus*, the more typical members of the Teleosts, the position, origin, insertion, and relation to the rami of the fifth nerve, of the muscle which I have identified as the pterygoideus are all such as to satisfy this identification completely.

In addition to this muscle there is, lying deep to it and also posterior and dorsal, one which a consensus of opinion, seemingly correctly, regards as the homologue of the elasmobranchian levator maxillae superior. The muscle in question is the levator arcus palatini. In the Chondrostei, the levator maxillae must be regarded as truly represented by the M. protractor hyomandibulae.

If these last identifications are correct then, clearly the pterygoideus muscle of the bony fishes cannot have been derived from the first levator also.

Still another objection to regarding the pterygoid as derived from the levator is the relation of the ramus maxillaris of the fifth nerve to the muscle in the amphibians. Always this nerve is superficial to the muscle. Since the levator maxillae superioris is placed entirely behind the fifth nerve in the elasmobranchs, it is difficult to understand how it can have found its way, not only in front of the nerve but deep to it, in its alteration to become the pterygoideus. It may be pointed out that the ramus maxillaris is entirely a sensory nerve, and, therefore, not subject to transportation by any muscle to which, otherwise, it would have supplied motor twigs.

On the other hand, the relation of the muscle which I have identified as the pterygoideus in the elasmobranchs, to the branches of the fifth nerve is the same as that of the pterygoideus in the amphibians and remains constantly so in all the changing forms that have been passed in review in the preceding pages.

The ramus ophthalmicus profundus may pass forward either superficially to the muscle, or in rare instances deep to it, both in the elasmobranchs and amphibians.

The ramus maxillaris in every instance passes forward superficially to the muscle.

The ramus mandibularis either passes behind the muscle or it crosses superficially to it between origin and point of insertion.

The diagram (Fig. 93) is intended to illustrate the relation of the pterygoideus muscle to the maxillary ramus of the fifth nerve as the muscle changes its situation. A, represents three elasmobranchian situations for the origin and insertion of the muscle ; the nerve passes forward superficially to the muscle. In B, we have the muscle arising behind the orbit, but in front of and above the exit of the nerve, as in several amphibians. In C, we have illustrated the condition in the Axolotls ; the nerve has to run backwards beneath the muscle to reach its posterior margin, around which it turns in order to pass forward. In D, we have the pterygoideus medius and internus of the reptiles illustrated. In E, the temporo-masseteric mass is illustrated, lying superficially to the nerves. In F, the temporo-masseteric muscles deep to the pterygoideus externus are shown by the dotted lines, and the ramus maxillaris is indicated as running forward to the anterior margin of these and then turning back so as to curve around the posterior margin of the pterygoid muscle, as in C. This last illustrates the fact that the more superficial muscle is really deep to the nerve which, itself, is deep to the more deeply placed muscle.

It is of interest to note in this connection that in the Axolotl the posterior extension of the pterygoideus muscle is correlated with a posterior transportation of the proximal portion of the ramus maxillaris. This, instead of coursing straight forward, as it does in those amphibians in which the M. pterygoideus does not extend its area of origin back to the otic capsule, passes from the foramen prooticum first dorsad and caudad and then turns forward over the posterior margin of the muscle. Actually this means that the nerve passes first backwards and then curls dorsad around the inferior margin of the muscle in order to pass forward to its destination.

The significance of the partial division of the pterygoideus muscle into partes internus and externus in *Necturus*, its division into three parts in *Pseudotriton*, and the presence of a pterygoideus internus muscle in *Ichthyophis* will be discussed after the muscles have been described in the Reptilia and the Aves.

THE MUSCLES OF THE HYOID SEGMENT.

The dorsal muscles of the segment have been sufficiently discussed, but some further consideration of my interpretation of the ventral muscles is desirable.

Lightoller, apparently misled by Drüner, regarded the interhyoideus—M. ceratohyoideus externus—of the amphibians as an interarcual caducous muscle and dismissed it completely from his discussion of the amphibian ventral constrictors. This resulted in his acceptance of Drüner's identification of the fore part of the superficial ventral hyoid constrictor as the interhyoideus.

I have shown that the " cerato-hyoideus externus " is a hyoid muscle, that it develops from the hyoid muscle plate, and has, in the 13 mm. larva of the Axolotl, no relation to any other than the hyoid segment. Norris and others have shown that the muscle is innervated only by the seventh nerve. The muscle is not caducous, but persists as a functional muscle in the adult of every amphibian in which it is developed.

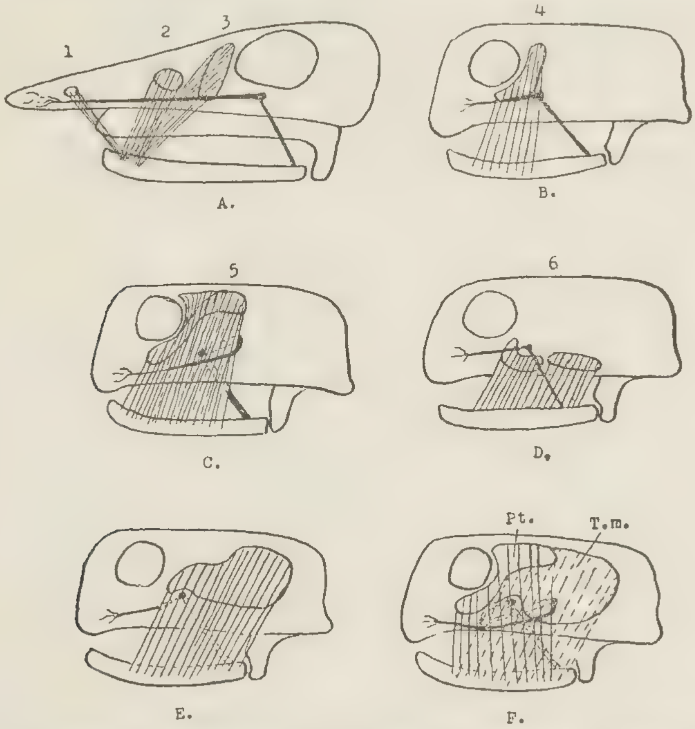


Fig. 93.—A diagrammatic presentation of the relation of the muscles of mastication to the branches of the fifth nerve.

I have found, further, that the primitive origin of the superficial constrictor of the hyoid segment is not in any part from the ceratohyoid, as in the adult, but entirely from the subcutaneous tissues dorsal to the upper end of that cartilage and along a line which commences in front of and ends well behind that upper end. The origin of the anterior part of the muscle from the ceratohyoid in the adult and older larvae is a secondary origin.

Unquestionably the appearance of the anterior part of the Csv.2, that which Lightoller and I designate Csv.2a, is very much, if not exactly, that of the interhyoideus of the elasmobranchs, but, it is believed, this resemblance is a parallelism and not a true homology.

In *Notophthalamus* the division of the Csv.2a into a pars superficialis and pars profunda, the latter arising in part from the cerato-hyoid cartilage, and running obliquely forward deep to the Csv.1, makes the resemblance to the elasmobranchian condition more perfect.

It is noteworthy that in the earliest stages no part of the ventral hyoid musculature arises from the ceratohyoid cartilage, that in this stage—the 13 mm. larva of the Axolotl—the superficial constrictor sheet is quite continuous, and the interhyoideus, deep to it, arises from the tissues close to the dorsal end of the ceratohyal. In all the adult urodeles studied one finds the anterior part of the constrictor sheet passing deep to the posterior end of the mandible to gain an attachment to the dorsal end of the ceratohyal, whilst the dorsal end of the interhyoideus has been forced, or has moved, back to gain an attachment to the dorsal end of the thyreoid cartilage, developed from the last branchial cartilage.

Comparison with the muscles in the Anura seems to lend further support to the identification of this anterior part of the superficial constrictor as the interhyoideus. In these forms the muscle which Gaupp designates the subhyoideus, and which is correctly identified as the interhyoideus by Lightoller, is developed from a muscle which, in early larval stages, arises from the ceratohyal cartilage on each side and meets its fellow in a mid-ventral raphe. There can be no question that this is a veritable interhyoideus.

But the position is complicated by the fact that there is no muscle developed in the Anura which may be identified as the superficial constrictor.

In these amphibians the Csv.1 presents three very definite parts, (1) a submentalis, and (2) an intermandibularis posterior, whose fibres are oblique to and underlie (3) a pars anterior, just as the anterior fibres of the Csv.2 underlie those of the Csv.1 in the urodeles. On the other hand, the fibres of the interhyoideus do not underlie the M. intermandibularis in the Anura.

The interhyoideus of the Anura, then, resembles the anterior part of the Csv.2 of the Urodela in its origin from the upper end of the stylohyal, but differs in that it does not gain an insertion deep to the Csv.1.

In the Anura there is no cerato-hyoideus externus.

It is surely only reasonable to conclude that there is no cerato-hyoideus externus, because the muscle deep to the constrictor which gives rise to it in the urodeles has here given rise to a superficial constrictor.

Again, in the Anura the superficial hyoid constrictor sheet is one muscle, and one only, whereas in the Urodela the constrictor sheet is always sharply divided into two, recalling the partes arcuata and inscriptionalis of the elasmobranchs.

Lightoller has suggested that the cerato-hyoideus externus may be, in part, a ventral extension of the pars quadrato-hyoidea of the Csd.2. Whilst the origin, dorsal to the midlateral line, supports this suggestion, it may be said that there is no evidence in its development to indicate a duality in its composition.

Finally, if the cerato-hyoideus externus be not homologous with the interhyoideus of the elasmobranchs and with portion of the protractor hyoidei of the bony fishes, then it must be regarded as an entirely new muscle. In view of its large size and importance functionally, this does not appear a reasonable interpretation. It seems more reasonable to regard it as a muscle inherited but modified.

Appendix.

The Laryngeal Muscles of the Amphibians.

Mixophyes Tadpole. (Fig. 94.)

The laryngeal muscles here described are those of a tadpole of full size, but before the formation of the pectoral limb girdle. It is the same as the youngest stage of which the cephalic musculature generally was described.

For the study of these muscles, the larva was cut transversely behind the branchial cavity and all the structures were carefully dissected off the posterior wall. The heart and pericardium were then removed. The whole branchial structure was then freed from the cranium dorsally, and opened along the mid-dorsal line. It was now found possible to cut free the posterior part of the basket and remove it completely. This portion was then stained and studied, after clearing and mounting in canada-balsam, spread right out flat.

The Dorso Laryngeus (D.l.) reaches the larynx, coming from above and laterally to it, behind the most posterior fibres of the constrictor pharyngei. Just before the muscle reaches the outer margin of the sphincter laryngei it turns on its edge so that the most anterior fibres reach the dense procartilaginous tissue surrounding the laryngeal aperture on the dorsal surface thereof and along the anterior half of the length of the slit-like closed aperture. To reach this insertion the fibres pass dorsally to and in front of the anterior half of the sphincter.

The Constrictor Pharyngei (C.ph.) apparently acts as a subsidiary dilator of the larynx. A posterior fasciculus of its fibres diverges from the rest of the muscle a little distance above and behind the larynx and passes to the anterior and deeper edge of the sphincter, and the fibres are inserted into the same raphe to which the fibres of that muscle are inserted. Actually, right at their termination these fibres are in series with those of the sphincter.

The Sphincter Laryngei (Sph.) would perhaps be better termed a laryngeus ventralis. The muscle is in two halves ; each arises in the mid-line behind the larynx and curves round it to be inserted into a raphe in the mid-line in front. The posterior raphe is exceedingly thin, so that it is only under higher magnification than one uses for dissection that one discovers the interruption in the continuity of the fibres. The anterior interruption, on the other hand, is quite an obvious gap between the two muscles. It is this division into two halves which suggests that this is really a laryngeus ventralis and not a true sphincter.

The division of the muscle strongly suggests that it is derived from two muscle plates, and, as it is a ventral muscle, the suggestion presents itself that it is a ventral " rest " of a fifth branchial segment.

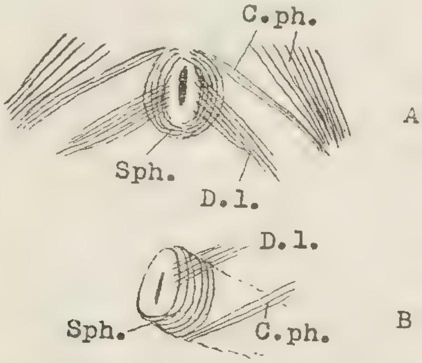


Fig. 94.—*Mixophyes* tadpole, stage C.—The laryngeal muscles.

Necturus.

The Dorso-laryngeus and the Constrictor pharyngei are as in the Axolotl, except that the latter lies entirely dorsally to the larynx and trachea, meeting its fellow in a median raphe above the trachea behind the larynx.

The Laryngeus Ventralis is a triangular little sheet of muscle which arises from the fascia behind the constrictor pharyngei and ventrally to the dorso-laryngeus. At its origin the muscle is very narrow, but as it passes mediad and rostrad towards the mid-line its fibres radiate and are attached to the dorsal edge of the arytenoid cartilage beneath the median end of the fibres of the dorso-laryngeus.

This last muscle is peculiar and unlike any other amongst the many forms studied.*

Its point of origin is quite a distance from the mid-line ; actually it is at about the junction of the middle and median thirds of the distance between the mid-line and the margin of the last branchial cartilage.

The Sphincter Laryngei is a very small muscle, just a few fasciculi which arise from a dorsal raphe at the anterior end of the arytenoid cartilages and pass round to be inserted beneath them, but not meeting in a median raphe ventrally.

Amphiuma.

I have not been able to dissect *Amphiuma* ; the following description is based upon a study of several excellent sets of serial sections. For these my grateful thanks are tendered to Professor H. W. Norris. These sections formed portion of the material Professor Norris worked on when he wrote his account of the cranial nerves of *Amphiuma means* (1908). There are several sets of transverse sections and one very fine set of sagittal sections. Whilst it was not found possible to determine the whole cephalic muscular anatomy with sufficient certainty that it was entirely correct, this want of certainty does not apply to the description of the laryngeal muscles except as to the origin of the two sheets which are inserted dorsal to the larynx.

---

* This condition recalls that of the 7 mm. larva of *Limnodynastes peronii*. Here the posterior fibres of the sphincter appear to be inserted into the loose connective tissue on each side of the larynx a little distance from it ; it also resembles somewhat the thyreo-arytenoideus ventralis of the adult *Hyla*.

The laryngeal muscles of *Pseudotriton* and *Siren* are essentially similar to those of the Axolotl except that, according to Wilder (1891), in *Siren* the laryngeus ventralis is a longitudinal muscle.

The structure of the arytenoid cartilage is more complex than in other amphibians.

The anterior tip of each cartilage lies alongside of the laryngeal fissure and is here a thin rod of fibro-cartilage ; a little further back it becomes flattened, and extends more deeply. This added depth is of hyaline cartilage. A ridge next appears on the outer side of the hyaline portion so that the cartilage comes to be triangular in cross section. The ridge rapidly subsides again posteriad, but almost at once the cartilage divides into a ventral and a dorsal arm. The ventral is the shorter and is formed entirely of hyaline cartilage, and tapers to a point rapidly. The dorsal, fibro-cartilaginous, arm is continued backwards and fuses with a succession of tracheal cartilages whose separate identity is manifested only by the fact that they project slightly both dorsally and ventrally around the trachea, but fail to meet in the mid-line either above or below.

In the 51 mm. larva the laryngeal muscles are very simple. A laryngeus dorsalis reaches the larynx from an origin high up on the fascia dorsalis and its fibres pass rostrad and ventrad to their insertion into the connective tissue condensation around the larynx close to the dorsal margin of the embryonic cartilaginous arytenoid. The Constrictor pharyngei has a dual origin : the more dorsal is from the deep, subdermal fascia immediately behind and lateral to the dorsal tip of the last branchial cartilage, the more ventral is from the dense connective tissue behind the tip of that cartilage. The fasciculi from these two origins meet behind and medially to the last cartilage and are continued mediad to be inserted into a mid-ventral raphe ventrally to the larynx and trachea.

The laryngeus ventralis and constrictor laryngei are both present ; neither extends more than half-way round the larynx.

In the adult the same muscles are present but they have been rearranged.

The Dorso-laryngeus arises from a connective tissue condensation which is situated a little higher than, and just behind, the tip of the last branchial arch. From above this point, there radiate dorsad the fibres of what is probably a pars dorsalis of this muscle, the appearance being very much that of the pars dorsalis of the muscle in *Ichthyophis*. From its origin behind the last branchial cartilage, the dorso-laryngeus passes rostrad and ventrad. The muscle is somewhat broader than that of *Ichthyophis* and also stouter. The more posterior fibres are inserted into the ridge of the arytenoid, but the great bulk of them are collected into a rounded muscle which courses forward alongside of the dorsal edge of the cartilage just above the ridge till the most prominent point of it is reached, when the muscle tapers suddenly and is inserted into that point.

In sagittal sections this muscle is very definitely divided into a dorsal and a ventral bundle of fibres between its origin and insertion, and it is believed that the more posterior fibres are those which, behind their insertion, are gathered together to form the ventral bundle. This suggests that there is here a dilator laryngei, as in *Ichthyophis*, but the fibres are so completely devoid of any dividing fascial or perimysial plane at both origin and insertion that it is not possible to assert the duality of the muscle.

The Constrictor Pharyngei is a thicker and broader muscle than the dorso-laryngeus. It arises behind and below the other from the connective tissue around the dorsal end of the last branchial cartilage. It is not nearly so broad a sheet of fibres as is the muscle in the Axolotl, being more like that of the adult *Amblystoma*, though relatively thicker. The insertion is into a mid-ventral raphe below the larynx and anterior end of the trachea. Its course is parallel and ventral to the dorso-laryngeus, but its anterior fibres reach forward only so far as the posterior margin of that muscle, whilst the posterior fibres are placed further back. I do not find any fibres of this muscle to have an insertion other than into the ventral raphe.

The Sphincter Laryngei.—The fibres of this muscle arise from a median raphe dorsal to the larynx, commencing immediately behind the apex of the lateral ridge of the arytenoid cartilage. They are placed between the longitudinal portion of the dorso-laryngeus and the cartilage as they pass around the larynx to be inserted into the mid-ventral raphe between the larynx and the constrictor pharyngei. These fibres have a slight inclination caudad from above down.

The Laryngeus Ventralis.—This name has been applied to a well differentiated muscle anterior to the sphincter. Its fibres arise from the mid-ventral raphe in front of the constrictor pharyngei. They pass dorsad with a slight inclination caudad to be inserted into the submucosa on each side of the larynx.

Amblystoma. (Fig. 95.)

The Arytenoid cartilages are simple, elongated plates of cartilage enlarged at the anterior end.

The Dorso-laryngeus (D.l.) and Constrictor Pharyngei (C.ph.) have already been described. Suffice it here to say that the dorso-laryngeus curls dorsad, just as it reaches the lateral margin of the sphincter, in order to reach the dorsal edge of the tip of the arytenoid cartilage in front of that muscle, where it is inserted.

The Sphincter Laryngei (Sph.) presents a relatively wide interval between its two halves dorsally ; ventrally they meet one another at the mid-ventral raphe.

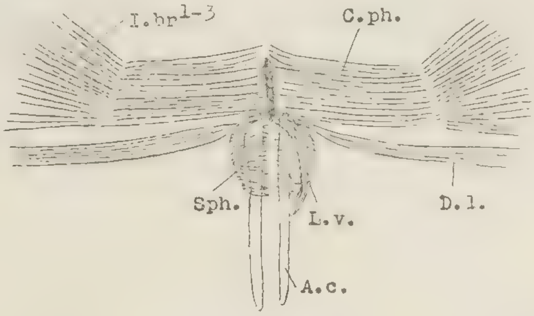


Fig. 95.—*Amblystoma.*—The laryngeal muscles.

The Laryngeus Ventralis (L.v.) arises from the mid-ventral line below the anterior margin of the sphincter and winds round the outer surface of that muscle from in front caudad and dorsad, to be inserted into the arytenoid cartilage behind the sphincter.

In this amphibian, as in *Hyla*, there is a deep slip of the rectus abdominis which takes its origin anteriorly from the submucosa a short distance posterior to where the dorso-laryngeus leaves the ventrum of the pharynx to pass dorsally and laterally beyond it. This slip recalls, strongly, the so-called interbranchialis 4 of the Caecilians.

In the 13 mm. larva it is not possible to recognize a laryngeus ventralis differentiated from the sphincter.

In the well-grown Axolotl the laryngeus dorsalis—dorso-laryngeus—is a wider sheet of fibres and it lies for the most part ventrally to the larynx and trachea. A few fibres, comparable in number to those present in the adult muscle, along the anterior border of the muscle only find their way to the dorsal edge of the arytenoid cartilage in front of the sphincter.

Molge.

The Constrictor Pharyngei (Fig. 96) is here reduced to an oval strand of muscle fibres which pass around the lateral fornix of the pharynx and across its floor to reach the ventrum of the larynx. Here the fibres are spread out just sufficiently to permit of the formation of a complete muscular layer below the larynx and are inserted into a mid-ventral raphe. Just where the muscle reaches the ventrum of the pharynx it is interrupted by a tendinous intersection, very similar to that which interrupts this muscle in *Amblystoma*. It is exceedingly fine and only visible when the dissected muscle is viewed by transmitted light after staining and clearing.

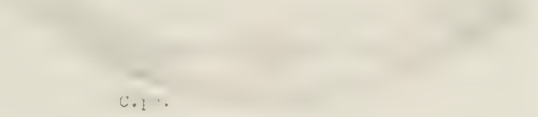


Fig. 96.—*Molge.*—The laryngeal muscles.

The Dorso-laryngeus passes from its origin alongside the last muscle till it has almost reached the larynx. It now leaves the other muscle, turning dorsad and very slightly rostrad, passing across the anterior face of the sphincter laryngei, and is inserted into the anterior end of the arytenoid cartilage near its dorsal edge.

The Sphincter Laryngei arises from the mid-ventral raphe below the larynx and curves round it with an inclination rostrad to be inserted into a mid-dorsal raphe above it. A bundle of these fibres appear to have a slightly more oblique direction than the others, to be inserted a little distance from the mid-line amongst the connective tissues beneath the mucosa. These perhaps represent a Laryngeus Ventralis muscle.

Ichthyophis. (Fig. 97.)

The muscles of the larynx in the adult *Ichthyophis* are slightly different from those of the larva, as described by Norris and Hughes. They have already been briefly described.

The Hyopharyngeus internus (C.ph.) has been already described as the homologue of the constrictor pharyngei (transversus ventralis 4). This muscle is perforated by the larynx. It arises from the median edge of the last branchial arch and its fibres are inserted into a median raphe, except where they are attached to the larynx or trachea as that passes through the muscle. The anterior fibres have a direction mediad and caudad at a sharp angle; the most posterior pass almost directly mediad, with only a slight inclination caudad.

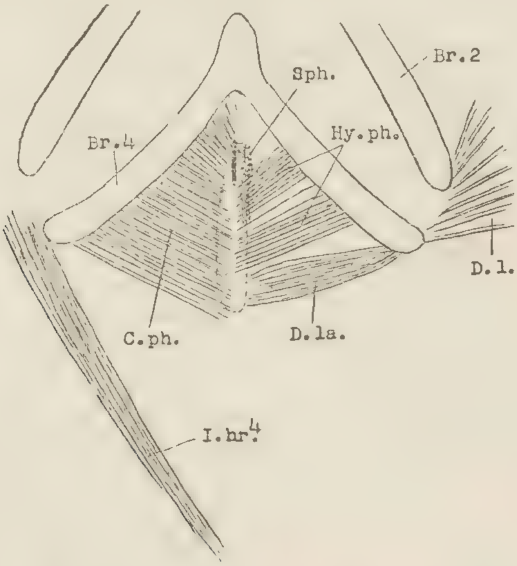


Fig. 97.—*Ichthyophis.*—The laryngeal muscles.

The most anterior fibres are in front of and ventral to the larynx; those next to these are inserted into the arytenoid cartilages as they penetrate the muscle obliquely from in front caudad and ventrad, behind these the fibres are inserted into a median raphe dorsal to the trachea.

The Hyopharyngeus (Hy.ph.) has been identified as the pars ventralis of the dorso-laryngeus. The muscle lies entirely dorsally to the larynx and trachea. Its fibres arise from the same edge of the last branchial cartilage as the last muscle and pass obliquely caudad and mediad to be inserted into a mid-ventral raphe dorsal to the trachea and larynx. These fibres are imperfectly divided into posterior and anterior portions, the latter arising from the more central, or ventral, the former from the more lateral, or dorsal, portion of the branchial arch.

The Dilator Laryngis (D.la.) arises from the tip of the last branchial arch and pass mediad with a slight inclination rostrad to be inserted into the arytenoid cartilage towards its posterior end. In the adult, this muscle lies posterior to, and is not overlapped by, the hyopharyngeus ventrally, but it would appear that such an overlap is present in the larva. It is possible that this is a specialized portion of the Dorso-laryngeus pars ventralis.

The Sphincter Laryngei (Sph.).—I have adopted this name rather than increase the synonymy of these muscles, but as it is not a continuous circular muscle the name is probably incorrect. Constrictor laryngei would be more appropriate.

The muscle is in two halves; each half arises from the strong connective tissue ventral to the larynx and curls round it to reach its fellow in a mid-dorsal raphe. The ventral gap between the two muscles is, as in *Mixophyes*, quite appreciable.

The Laryngeus Ventralis, which Norris and Hughes describe in the larva, is not distinguishable in the adult. This has been determined, like all the other features of *Ichthyophis*, by careful comparison of the entire specimen and the serial sections.

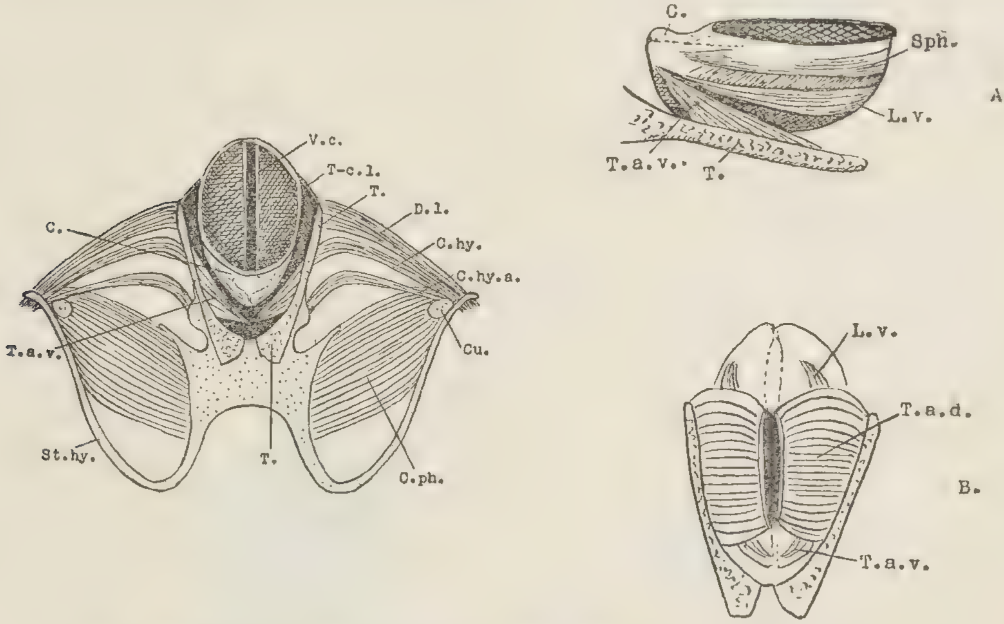
Whilst it proved possible to dissect all the muscles described, the dissection was further checked by separating the whole of the muscles, together with the larynx and anterior part of the trachea and ventral laryngeal mucosa, and then, after staining and clearing, studying them again.

The " Interbranchialis 4 " (I.br.) which Norris and Hughes describe in *Herpele* is present in the adult *Ichthyophis*.

Hyla. (Figs. 98, 99.)

The three ptery-hyoid muscles and the Constrictor Pharyngei have already been sufficiently described (p. 184).

The arrangement of the remaining muscles is quite unlike any that have been previously described, and the identification of the muscles of those simpler forms in this complex laryngeal mechanism is by no means a simple matter.



Figs. 98-99.—*Hyla*.—Laryngeal muscles. C., Cricoid cartilage; T.a.d. & T.a.v., Mm. thyreo-arytenoideus dorsalis and ventralis; T-c.l., Thyreo-cricoid ligament; V.c., Vocal cords.

The Sphincter Laryngei (Sph.).—This name is applied to a muscle which almost completely surrounds the larynx towards the ventral edge. The muscle arises from the perichondrium of the arytenoid cartilage a little behind the anterior end thereof, and is inserted into a median raphe posteriorly. The muscle is incompletely divided into two portions; some of the dorsal fibres arising anteriorly are inserted into the perichondrium a short distance from their origin, whilst some of those inserted into the posterior raphe do not extend quite half-way towards the anterior origin of the muscle, but are inserted like the short anterior fibres.

The Laryngeus Ventralis (L.v.) arises from a median raphe anterior to the larynx and passes around it dorsally to the Sphincter to be inserted into the median posterior raphe.

The Thyreo-arytenoideus Ventralis (T.a.v.) arises in common with the laryngeus ventralis. Its fibres pass caudad and dorsad to be inserted along the median and ventral margin of the ossified thyreoid cartilage.

The Thyreo-arytenoideus Dorsalis (T.a.d.) arises from the median and dorsal edge of the thyreoid bone and passes dorsad and mediad to be inserted on to the lateral surface of the arytenoid cartilage above the laryngeus ventralis.

To attempt the identification of these muscles without detailed knowledge of their development is to some extent speculation, but there is evidence which justifies the speculation, and seems to indicate that the nomenclature adopted is probably correct.

It is necessary, first of all, to recognize that the anterior end of this larynx is the ventral end of the more simple larval larynx, and that the dorsal surface is the posterior end.

With this recognized, one cannot but remark that the dorso-laryngeus of the branchiate amphibians is inserted on to the arytenoid cartilage in front of the constrictor laryngei. We further recall that we have had reason to believe that the dorso-laryngeus is interrupted at the tips of the branchial cartilages in the caecilians.

With these facts in mind, one suggests that the dorso-laryngeus in *Hyla* has been interrupted at the thyreoid cartilage and that its pars ventralis is the muscle which has been designated the thyreoarytenoideus dorsalis, its pars dorsalis being that which has been designated the dorso-laryngeus.

The laryngeus ventralis is here thought to have been divided into laryngeus ventralis and thyreo-arytenoideus ventralis.

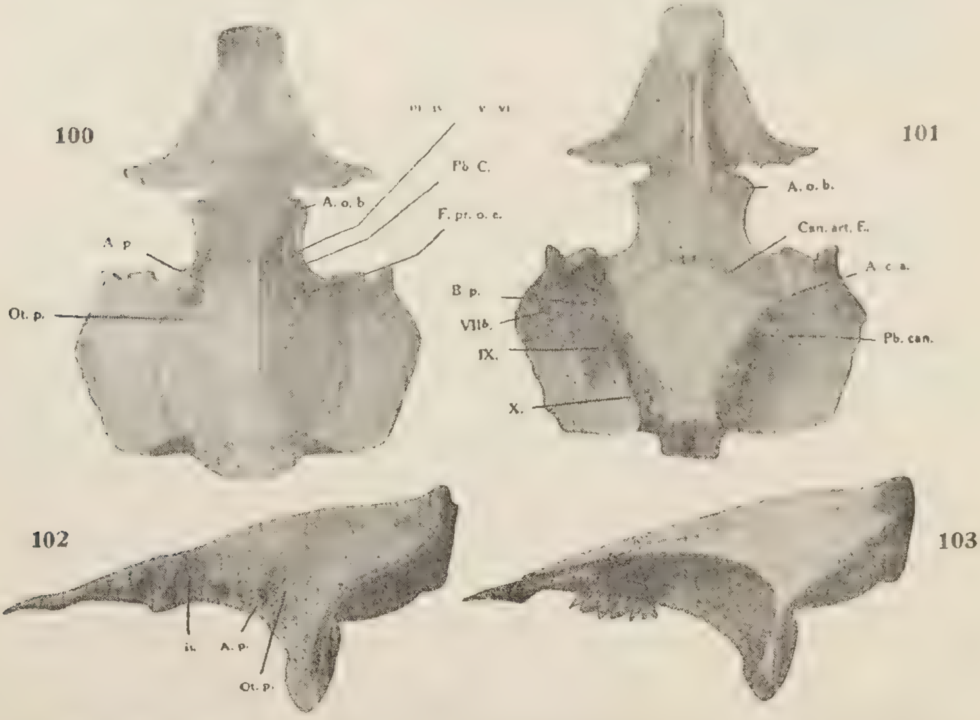
In view of the fact that in the tadpole, prior to metamorphosis, a few of the posterior fibres of the constrictor pharyngei are intimately related to the antero-ventral portion of the larynx, there is justification for suggesting that the cranio-hyoideus and cranio-hyoideus anterior are portions of the constrictor pharyngei.

THE SKULLS OF THE AMPHIBIANS.

1. The Dipnoi.

The skull of the dipnoans is peculiar by reason of the very complete retention of the cartilaginous case in the adult, more complete than, and more massive than, even any elasmobranch presents us with.

That of *Neoceratodus* was very fully described by myself in 1931, and that of *Lepidosiren* by Bridge in 1893. It is believed that the reproduction of the illustrations which accompanied those descriptions is sufficient for the present purposes (Figs. 100–109).



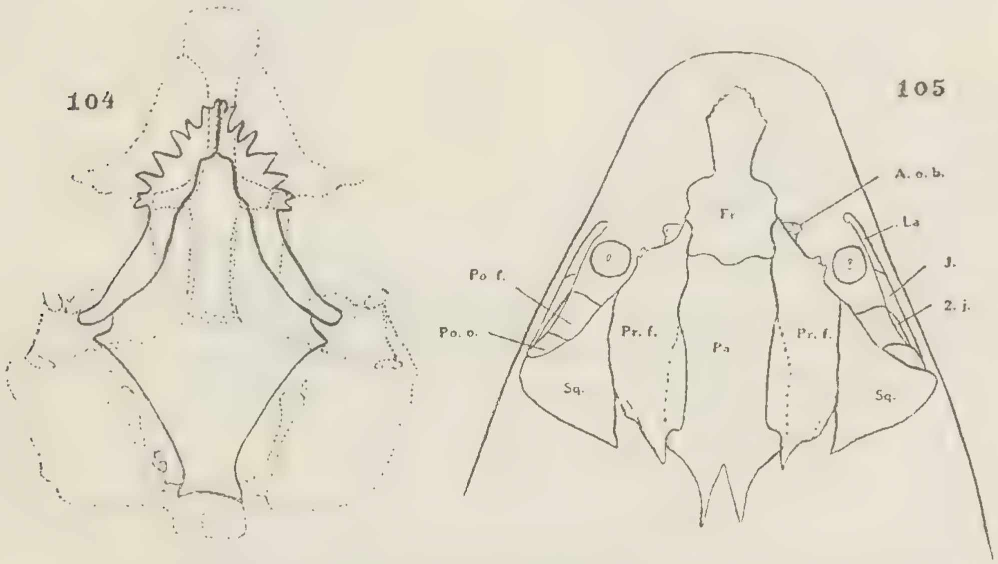
Figs. 100-103.—*Neoceratodus*. Figs. 100-102. Three views of the chondrocranium. Fig. 103. Side view with the dermal bones in place.

Before proceeding further, however, it will be convenient, with these illustrations before us, to discuss the significance of the three big bones on the base of the skull and that on the side of the skull which I identified as the squamosal bone.

The parasphenoid, lying upon the base of the skull in the middle, is at once recognizable. As compared with that of the fishes, it is markedly reduced. The lateral wings, which are of almost universal occurrence in the fish skull, are missing.

On either side of the parasphenoid is the bone which has been designated pterygo-palatine. These occupy essentially the position of the pterygoid bones of such reptiles as the chelonians and cotylosaurians. When compared with the fishes, the three bones together will be observed to occupy almost the position of the parasphenoid.

The designation pterygo-palatine is either one of convenience, a cloak to cover ignorance, or it is an implication that we have here a bone which is a combined palatine and pterygoid. Whilst the evidence in favour of a palatine component is far from convincing, its situation and its manner of development, as a membrane bone applied to the base of the skull, are, it is believed, sufficient to satisfy all the demands of an identification as the pterygoid bone, homologous with that of the *reptiles* and embolomeran amphibians. The so-called pterygoid bone of all other *amphibians* develops as a membrane bone in relation to the palato-pterygoid arch, and may or may not make contact with the side of the base of the skull and the edge of the parasphenoid bone which covers that base.



Figs. 104-105.—*Neoceratodus*. Outlines of the bones, seen from above and from below.

Now, the dipnoan amphibians resemble the rest of the group in that the pterygoid bones make contact with the parasphenoid medially. This is a particularly interesting relation, because it at once suggests that the pterygoid bones are homologous in the two divisions of the group. The appearances here are entirely deceptive. There is, in the dipnoans, no palato-pterygoid arch or process, and the bones are developed quite differently. I would not willingly lay myself open to a charge of dogmatizing and, therefore, explain that the appearances are regarded as being "entirely" deceptive because, for me, the evidence of development outweighs mere adult topographical relations; since the pterygoid bone of the dipnoan amphibians develops differently from that of the remainder of the amphibians, it is deemed to be a different bone in the two groups.

This belief is further supported by the resemblance of the dipnoan bone to the pterygoid of many reptiles, both in the manner of its development and in the topographical relations in the adult. The topographical relations of the adult bone in the Embolomeri are much more nearly those of the reptiles than those of the amphibians, and in them the parasphenoid is probably entirely absent.

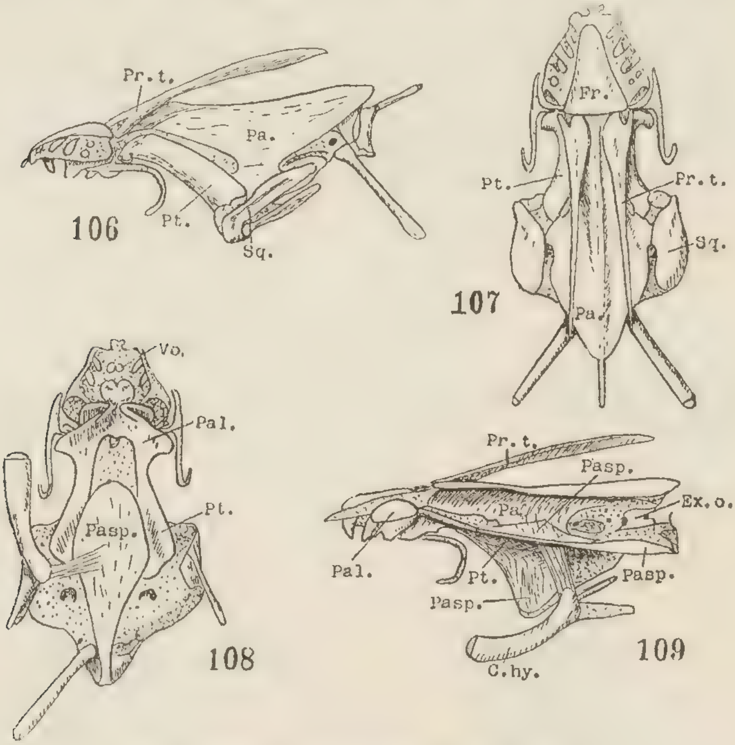
In the fishes, one seeks in vain for any bones which may be compared with the pterygoids of the dipnoans. One is, once again, struck by the fact that the parasphenoid of the fishes occupies the position of all three, so that one could readily reproduce the dipnoan condition by cracking free the lateral wings of the parasphenoid. Unquestionably, the lateral portions of the parasphenoid as seen in the fish have, in the dipnoans, been replaced by the pterygoids.

The question now arises: Is this a replacement by some other element, or is it the result of the failure to fuse of three centres of ossification of the complete bone?

The latter seems the more probable explanation; it is simple and calls for none of the complicated series of changes which must have preceded replacement by some other element.

What were those complicated changes?

Firstly, it could be assumed that the replacement was by an entirely new centre of ossification. The possibility of this is at once admitted, but if this new centre developed on an already fully encased skull, it is difficult to understand why it should have arisen. On the other hand, if it appeared at the lateral edge of the parasphenoid on a largely cartilaginous skull, why should it have invaded an area already adequately protected by the parasphenoid, and in doing so surely introduce instability into an area of bone to which important muscles of mastication were almost certainly attached?



Figs. 106-109.—*Lepidosiren* (from Bridge, 1898).

Before passing to consider another possible method of replacement it should be noted that a "new centre" hypothesis must imply a homology with the pterygoids of the remainder of the amphibians.

A second possibility is to assume that one of the bones of the palatal arch has come to occupy this situation.

In the fishes, with the exception of the Holocephali, the palate is hung to the skull by the hyomandibular bone or cartilage.

The Holocephali themselves, in a number of features, provide the evidence that the inception of the monimostylic suspension, characteristic of the amphibians, antedated the development of the piscine bony palate, possibly without any stage of hyoid suspension. If we grant that the evidence under this head is inconclusive, it is still difficult to accept the theory that one of the bones of the palatal arch has migrated back and taken up this position on the base of the skull, as against the more simple explanation of the origin of the bone by the splitting of the parasphenoid.

There are no recognizable transitional stages in the progression of the palatal element. Therefore, if we adopt this hypothesis, it is left to our imagination to decide whether we prefer to believe that the palatal element became attached to the base of the skull anteriorly and grew backwards, or that it, in effect, crawled up the mandibular arch and became attached posteriorly and then grew forward.

If the bone is to continue to be regarded as the homologue of the pterygoid of the remainder of the amphibians, except the Embolomeri, one or other of these hypotheses must be accepted. Some workers may elect to make the choice, but for me it appears a useless and fruitless exercise of the imagination.

There is, in my mind, little room for doubt that the pterygoid bone of the dipnoans is homologous with that of the embolomeran amphibians and with that of the reptiles, and in these we can see the reduction of the median remnant of the parasphenoid.

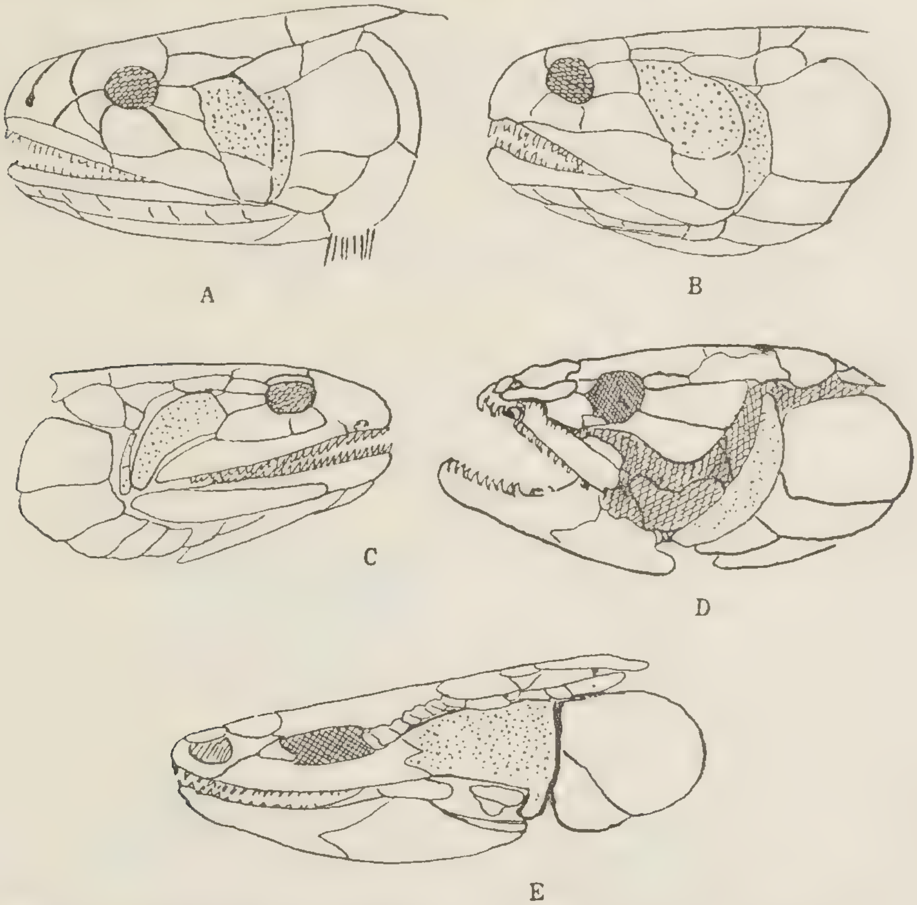


Fig. 110.—A, *Megalichthys*. B, *Rhizodopsis*. C, *Osteolepis*. D, *Amia*. E, *Polypterus* (from Wellburn and Gregory, Traquair, Gregory and Allis).

Entering the realms of pure speculation, one could offer a possible mechanical explanation of the gradual extinction of the central portion of the parasphenoid bone by the mediad growth of the lateral portions, once the bone had been split, and indeed this may also explain why it was so split.

The deeper portions of certain of the muscles of mastication are, and probably were, attached to the lateral area of the ventral surface of the parasphenoid. It is at least possible that, by early attachment to the perichondrium, these muscles penetrated the ossific membrane and determined a line which was not so readily ossified, and in time split the bone into three parts. Once the bone was split it is, at least, not unreasonable to suppose that, with increasing strain on the origin resulting from increasing size and strength of the muscles of mastication, there would have been increased need of strong attachment of the bone of origin to the skull. This need could have been met by increased area of attachment of the bone to the skull.

In conclusion, it is believed that the pterygoid bones of the dipnoan and embolomeran amphibians are homologous, on the one hand with the lateral wings of the parasphenoid bone of the fishes, and on the other with the pterygoid bone of the reptiles, and that the so-called pterygoid bone of the remainder of the amphibians is not homologous with these.

The squamosal bone of the dipnoans is of interest as an important link in the probable evolution of the tetrapod bone from one of the bones of the cheek armature of the fishes.

In *Neoceratodus* the bone presents a dorsal squame, which is in series with the other subdermal bones that form the roof of the temporal fossa, and a descending limb which is fitted to the upper surface of the quadrate cartilage. The homology of this bone with those of the higher vertebrata was, it is believed, sufficiently established in the communication of 1931. At that time it was not known that the bone in *Neoceratodus* resembles completely that of such anuran forms as *Bufo* and *Calyptocephalus*.

Before proceeding further, I would stress again a point of view stated previously (1931, p. 256) : " Any attempt to homologize the cranial elements of the fishes, dipnoans and [other] amphibians can only be made under the assumption . . . that, having evolved from a common ancestor, the same inherited [evolutionary] potential produced the same cranial elements in all."

This attitude permits one to discuss and suggest homologies in various forms without, of necessity, implying that any of the elements are derived directly from any other.

It appears probable that the squamosal of the tetrapods has been evolved by the modification of a bone comparable to the preoperculum of the fishes, with, perhaps, the addition of one or two of the cheek plates in front of it.

In Figs. 110 and 111, I have arranged a series of side views of skulls to convey my ideas in this connection. The squamosal and its assumed homologues have been stippled in each drawing.

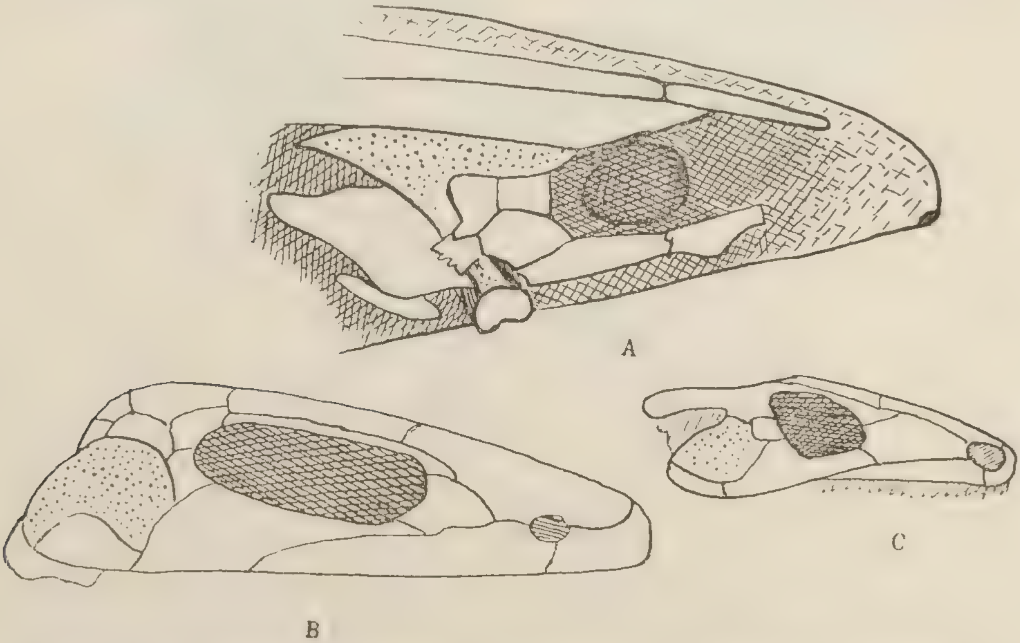


Fig. 111.—A, *Neoceratodus*. B, *Loxomma*. C, *Seymouria*. (B and C from Embleton and Atthey, and Gregory.)

The fish bone from which the squamosal is deemed to have been derived is that one of the cheek plates which was attached to the quadrate and hyomandibular. So long as the hyomandibular remained this bone gained only fibrous or no attachment to the skull. Any attachment other than fibrous would have impeded the mobility of the hyo-cranial joint. When the hyomandibular was absent and the quadrate was firmly attached to the skull, the squamosal also gained attachment to the skull, whilst still retaining its relation to the quadrate. Both its position in the roof of the temporal fossa and its attachment to the quadrate are, then, primitive features and are preserved in *Neoceratodus*, some anurans, and a large number of fossil amphibians. Whether the subdermal roofing flange of the bone which is present in some chelonians and other primitive reptiles is a secondary growth or a persistent primitive feature it is not possible to say. In the great majority of the higher vertebrata, the quadrate-attached is the only primitive portion persisting, and to this have been added various expanded flanges which may or may not contribute to the completion of the cranial wall and roof.

Thyng (1906) demonstrated the close association of the squamosal bone and the quadrate cartilage in the embryonic mammal, a relationship which is explained by the foregoing suggestions.

2. The Skulls of the Euamphibia.*

The Skull in the Anura.†

(Figs. 112–114.)

In several features the skull of the Anura is more primitive than that of any other amphibian type. Of these, two are outstanding: the platybasic "elasmobranchian" form of the cavum cranii and the form of the synpterygoid (parasphenoid) covering of the basis of the cranium.

The uniformity of the skull throughout the Anura is such that it were largely a waste of time to describe any one of them in detail; all are essentially similar to the much figured and described skull of *Rana*.

There is an extreme simplification of the ossific pattern of this skull as compared with that of the bony fishes. There are but two ossifications of the primordial cartilage on each side in the parachordal region, the prootic and the exoccipital, and in the trabecular region only one.

In the young skulls the two ossifications of the parachordal region are separate, not only from those of opposite sides but also from one another.

In the adult skull these four ossifications are completely fused and have in their extension encased the auditory capsule in one continuous mass of bone, in which no sutures are recognizable. Not only is this so, but the anterior, prootic, ossification has invaded the side wall of the cavum cranii in front of the incisura prootica, giving rise to a veritable alisphenoid lamina.

The ossification of the primordial cartilage in the trabecula region is more diffuse at its inception, so that it is hardly possible to regard it as a paired process. In the ultimate result there emerges a relatively extensive bone which encircles the cavum cranii. The antero-posterior extent of this area of ossification, the sphenethmoid bone, is subject to fairly wide variation. It may extend back sufficiently far to articulate with the anterior margin of the alisphenoid lamina of the parachordal ossification, the prootic, and it may extend so far forward as to contribute to the formation of the posterior walls of the nasal capsule. The full range of these variations is presented within the single genus *Hyla*, and cannot be regarded as being of any phylogenetic significance.

Of the covering bones, commencing with those on the ventral surface, the extensive synpterygoid, parasphenoid, is one of the most striking features of the skull. This large single covering bone of the basis cranii is found, elsewhere than in the amphibians, only in the fishes. Its presence is one of the primitive features of the amphibian skull.

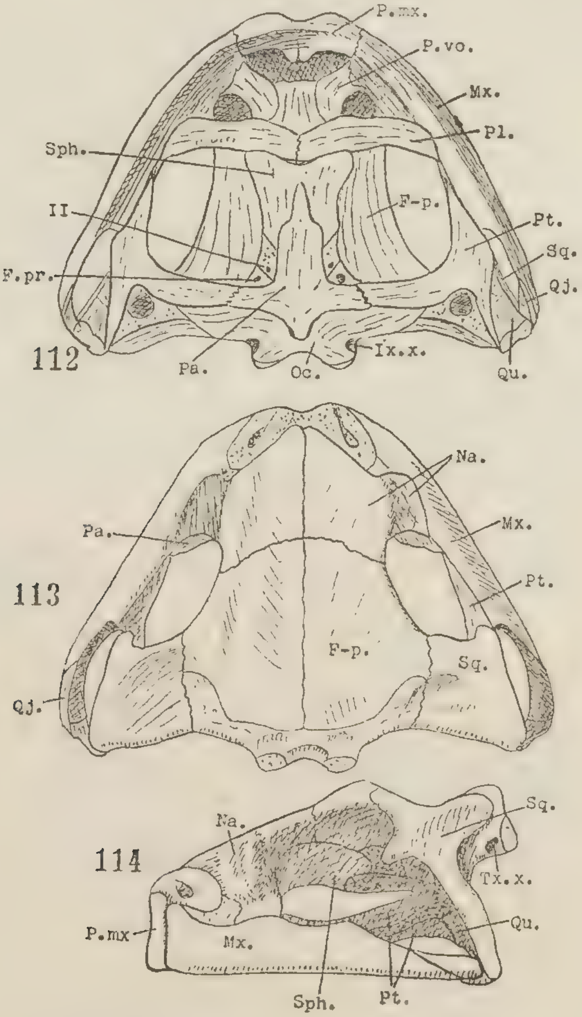
The palatine bones are developed along the posterior margin of the inferior surface of the lateral expansion of the ethmoidal cartilage behind the nasal capsules. Usually these are but narrow splints and are devoid of any palatal extension, but at times, and notably in *Pelobates*, they extend well over the palatal surface of the ethmoid cartilage and may even reach anteriorly to the internal nares. In no anuran skull do these bones articulate with one another at the mid-line, nor are they found between the nares.

---

[*] The term Euamphibia is used here, in a different sense from that in which it has been used in the past, to include the Anura, Urodela, Apodes and Stegocephalians, except the Embolomeri. A justification for this procedure is offered in section 3 of "Phylogeny of the Amphibia", pp. 232-236.

[†] It might have been thought advisable to deal first with those very ancient amphibians, the "Embolomerus" forms from the Lower Carboniferous rocks. They are, however, reserved till the end of the section, when it will be found that their peculiar specializations are such that they form a very fitting introduction to the section of the work dealing with the Skulls of the Reptiles. Not only is this so, but any discussion of the fossil forms must rest upon a knowledge of the recent, which, alone, we are able to dissect and to disarticulate and thereby determine beyond doubt the relations of the bones to one another and to the soft structures. For this reason none of the fossil forms will be discussed till the recent have been passed in review.

The Prevomers are of variable extent. Typically they are situated medially to the internal nares, supplying the medial and a large part of both anterior and posterior margins to those apertures. They may or may not articulate with palatine laminae of the maxilla. Occasionally these two bones articulate at the mid-line, and commonly they are articulated to the anterior margin or inferior surface of the anterior portion of the ethmoid; exceptionally, as in *Calyptocephalus gayi* (Parker, 1881) they articulate with the fore-end of the synpterygoid.



Figs. 112-114.—*Bufo* (from Parker, 1881).

The dorsum of the skull is more or less completely covered by two pairs of bones which have been designated fronto-parietals and nasals. In *Pelobates fuscus* (Parker, 1881) the four bones are fused to form a remarkable solid cuirasse, but in the great majority of instances the bones are quite separate and distinct.

The Fronto-parietals cover more or less completely the occipital and sphenoidal regions but may meet at the mid-line only over the former region, and in front thereof may diverge, leaving an area devoid of bony covering between their divergent ends and the posterior boundary of the sphenoid bone. The area in question is that of the dorsal fontanelle, and here the cavum cranii is enroofed by membrane only.

The Nasal bones are variable in their relation to the other pair of roofing bones and in their extent. Most typically they are developed around the anterior margin of the incomplete cartilaginous tectum nasi and spread forward over the nasal capsules. In this typical form the nasals are not in contact with any other bones. Extending further back, they come to lie in contact with the anterior portion of the sphenethmoid, and further backward extension leads to sutural contact with the anterior margin of the fronto-parietal. In, e.g. *Calyptocephalus gayi* and *Bufo* (Parker, 1881) the nasal bones are particularly extensive ; they extend forward almost to the margin of the external nares and backward, covering the sphenethmoid bone completely, to suture with the fronto-parietal, and then, expanding laterally, they make sutural contact with the ascending lamina of the maxilla. In *Bufo agua* the nasal bones extend back so far as to give the impression that in this form the skull is roofed by paired parietals and frontals and that, as in the Chelonia, the nasal bones are absent.

Actually the designation of the nasal bones is rather a matter of mutual agreement than of definite identification. There are no relations to any structures which permit one to assert that the bones would not be as correctly designated prefrontals as similar bones are designated in the Chelonians. The fronto-parietals occupy the area which the frontals and parietals in the reptiles occupy, but since we have no evidence of two centres of ossification, one only of those bones is really present. The decision as to whether the single bone is a parietal which has grown forward or a frontal which has invaded the region of the parietal is simply evaded in the designation adopted. It seems probable that, of the two alternatives, the former is the more likely. The nasal bones certainly appear to be placed too far forward to be regarded as frontals, but actually they do not, in the Anura, extend so far forward as the prefrontals of the Chelonia.

The Septomaxillary bone ossifies in membrane in relation to the dorsal surface of the solum nasi. There is some variation in its situation, but in the generality of instances it is placed at the posterior and lateral margin of the external naris. The bone is in all probability a true dermal roofing bone of the dorsal series and the homologue of one or other of the several present in the roof of more primitive vertebrates. It is not, however, possible to indicate which of those it does represent.

The so-called Pterygoid bone, which I would regard as the Os transversum, is a triradiate bone related to the inner surface of the posterior end of the cartilaginous maxillary arch, the ramus of the quadrate, and the antero-inferior surface of the auditory capsule. The homologies of this bone will be discussed at some length in a later section. For the present it will suffice to draw attention to the fact that it develops first as a membrane bone in relation to the posterior end of the cartilaginous maxillary arch (pterygoid process) and later grows backward to attain the adult relations. It is in sutural contact anteriorly with the posterior end of the maxilla, and, finally, it forms the anterior and median boundary to the space through which the muscles of mastication pass from their origin to reach the lower jaw. This space may be conveniently designated the via masticatoria, and in the Anura it is bounded medially by the " pterygoid ", laterally by the quadrato-jugal, and posteriorly by the quadrate and its encasing bones, the postero-lateral ramus of the " pterygoid " and the descending ramus of the squamosal, when that is present.

The Squamosal bone is particularly well developed in the genus *Bufo* (Parker, 1881), and in these forms it is strikingly similar to that of *Neoceratodus*. There is the same splint-like descending ramus on the antero-lateral surface of the quadrate, and an expanded dorsal body, which sutures with the fronto-parietal and contributes to the formation of an incomplete roof to the temporal fossa. The squamosal also, in the great majority of the Anura, contributes to the boundary of the tympanum dorsally.

The quadrato-jugal bone, probably more correctly designated quadrato-maxillaris, since no jugal bone is present, sutures only with the quadrate and the maxilla.

The prootic and alisphenoidal regions of the skull of *Hyla* will be found described with greater detail in a later section of this work dealing with the serial homologies of the Alisphenoid bone.

The facial and trigeminal ganglia lie partly within the cranial cavity on a depression on the floor of the cavity with the prominence of the anterior semi-circular canal behind and above the recess. Portion of the ganglia, however, protrudes through the foramen prooticum. In front of the foramen there is an alisphenoidal extension of the prootic ossification. This has arisen by extension of the ossification into the crista trabeculae from the otic centre, and is very definitely not contributed to in any way by an ascending process of the quadrate.

The alisphenoidal lamina is perforated by the foramen for the internal carotid artery. It will be observed that in the Urodeles and in the Apoda this carotid foramen is placed further back.

There is no bony or cartilaginous bar between the branches of the fifth nerve as they pass away from the incisura prootica.

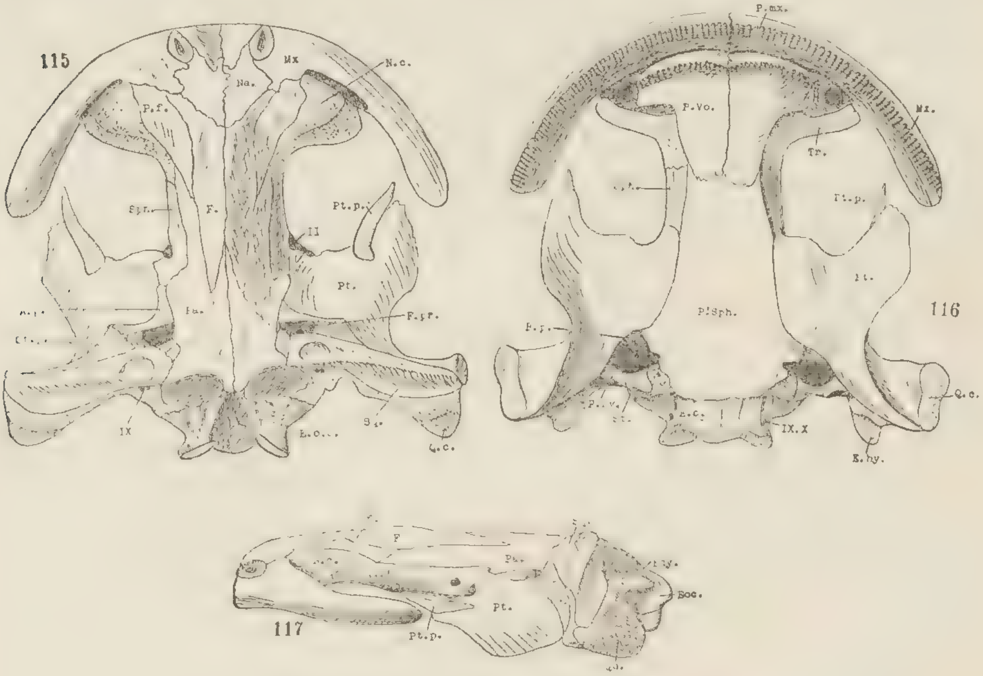
The Skull in the Urodela.

(Figs. 115–117.)

The endochondral ossifications of this skull are essentially similar to those of the Anura. The two ossifications, however, are less extensive, and the sphenethmoid is usually represented by paired bones which do not meet one another at the mid-line. They have been designated orbitosphenoids by some writers.

There are four pairs of dermal roofing bones, parietals, frontals, prefrontals and nasals.

The squamosal bone in the great majority of the genera is a simple splint applied to the lateral and dorsal surface of the quadrate ramus, but in exceptional instances is expended in the temporal roof and may make sutural contact with the parietal and with the frontal.



Figs. 115-117.—*Sieboldia* (from Parker, 1882).

The quadrato-jugal is absent, and, except in a few instances, in which the maxilla is extended far back, there is discontinuity in the maxillary arcade between the posterior end of the maxilla and the quadrate. In some forms the maxilla is reduced almost to complete extinction. The premaxilla commonly presents ascending processes which suture with the nasals between the external nares. The maxilla, when well developed, may suture with nasal, prefrontal and frontal, laterally to the external nares.

On the ventral surface of the skull the most extensive bone is the synpterygoid. This is not "T"-shaped as in the Anura, but tapers forward from its broadest point, below the auditory capsules, to its truncated anterior end. Actually the width of the bone is subject to greater variation than in the Anura; it is widest in such forms as *Cryptobranchus* and *Menopoma* and narrowest in the English Newt (*Molge*).

The Prevomers are very extensive bones. Developed at first in the same situation as those of the Anura, they, in late stages of larval and early adult life, grow backwards on either side of the mid-line, lying below the anterior portion of the synpterygoid.

The Palatine bone is evanescent. It appears in early stages of development in the situation of the palatine in the Anura but disappears later.

The "Pterygoid" bones are subject to very wide variation in their size. Again *Cryptobranchus* may be taken as one extreme and *Molge* as the other. In the former genus the bone bears resemblance to that of the Anura, but with the wide angle between the two anterior rami filled in and the bone extended forward to form an extensive floor to the temporal fossa. As in the Frogs the via masticatoria is bounded medially and anteriorly by this bone. In *Molge* the pterygoid is reduced to a short splint with an expanded base which lies upon the ventral surface of the pterygoid process of the quadrate. In the former genus the pterygoid sutures with the lateral edge of the synpterygoid for some distance, in the latter genus it sutures with no bone at all.

The development of the "pterygoid" is a matter of importance, as its homology with the similarly-named bone in the Embolomeri and Reptiles will be questioned later.

It may be stated that throughout the recent Amphibia the so-called pterygoid develops as an epichondral ossification in membrane in relation to the pterygoid process of the quadrate; later it extends so as to cover part of the ventral surface of the auditory capsule and to suture with the synpterygoid. Parker, very significantly, wrote of *Siren* (1882), "The suspensorium, having no pterygoid outgrowth, and no correlated pterygoid bone, is naked below", emphasizing this constant relation.

With but rare exceptions, the quadrate presents well developed ascending, otic and basal processes by which it is articulated to the otic and prootic region of the cavum cranii. The ascending process* rises in front of and lateral to the prootic foramen and fuses with the crista trabeculae. In the great majority of the genera the greater part, if not the whole, of the quadrate remains unossified, as also does the prootic portion of the crista.

The otic process* may or may not fuse with the upper part of the otic capsule; in the majority of genera the fusion is very complete.

The basal process is attached to the anteroventral and lateral corner of the otic capsule and is confluent with the ototrabecular bar in this position.

Immediately behind, and slightly above, the articular surface of the quadrate there is commonly a posteriorly projecting stapedial process with which the outer end of the stapes articulates.

Opposite the stapedial process there arises a pterygoid process of very variable length, absent altogether in some forms; in most it is continued forward close to the trabeculae, but lateral and ventral to them, to fuse with the antorbital cartilage.

The foramina for the exit of the fifth and seventh nerves are found on the inner side of the cranial cavity near the anterior end of the otic capsule.

The Gasserian ganglion lies entirely within the cavum cranii in a recess bounded by the otic capsule behind, the crista trabeculae in front, and the auditory and ascending processes of the quadrate laterally. Its three branches leave the cranium through the foramen prooticum. The maxillary and mandibular rami pass on their way posteriorly to the ascending process, whilst the ophthalmic division insinuates itself between the ascending process and the crista trabeculae, passing forward to the inner side of the process.

The geniculate ganglion lies, for the most part, within the cranial cavity though portion of it may be insinuated along the facial canal. This latter perforates the fore-end of the otic capsule, and through it the ramus hyomandibularis reaches the outer surface of the otic capsule behind the stapedial process of the quadrate. The ophthalmic branch of the nerve passes through the foramen prooticum along with the maxillary division of the fifth. The palatine division penetrates the floor of the cranium, passing close to or through the carotid foramen to reach the anterior division of that canal along which the palatine terminal branch of the vessel travels.

The Skull of the Caecilians.

(Fig. 118.)

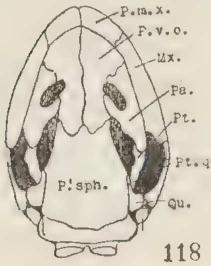
In their cranial characters the Caecilians present the same similarity one to the other that was observed in the Anura. In the complete cranial roof they present striking similarity to certain of the Stegocephali, and this similarity is also present in the palatal architecture, though not so markedly, and yet, perhaps, it is more genuine.

---

* Watson has confused these two processes; for he writes of the Upper Triassic Stereospondyls that they have "an otic process of the palatoquadrate cartilage, which articulates with the prootic region of the skull" (1919, p. 58). It is the ascending process of the Urodeles which articulates with the prootic region of the skull.

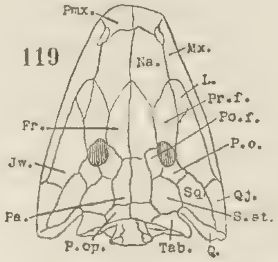
Apparently the endochondral ossifications are similar to those of other Amphibia, but their development is not so well known, so that it is not possible to speak confidently here.

As in the Urodela there are paired parietal, frontal, prefrontal and nasal bones, but they are of somewhat different proportions. The parietals and frontals are similar, but the prefrontals are smaller and the nasals larger. A closer examination, however, discovers that the parietal and frontal bones extend laterally beyond the cavum cranii and contribute to the formation of a temporal roof which is completed by an extensive squamosal. Except in one species of *Caecilia* the squamosal bone sutures with the frontal and the parietal, though in several the suture with the latter bone is interrupted by a narrow fissure posteriorly. The squamosal bone does not extend down the short quadrate ramus as it does in the Urodeles and Anura but reaches only the otic (?) root of the quadrate.

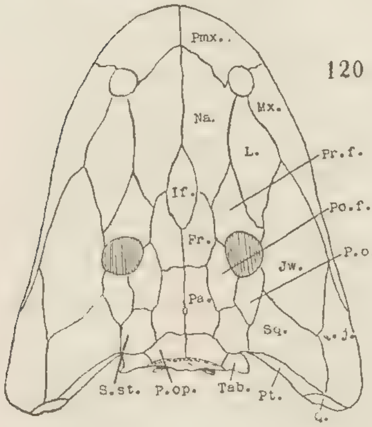


118

119



120



121

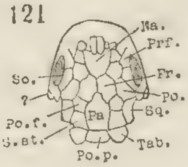


Fig. 118.—*Ichthyophis* (from Wiedersheim, but slightly modified to show more clearly the true relation of the os transversum to the pterygoid bone.)
Fig. 119.—*Capitosaurus* (from Zittel).
Fig. 120.—*Eryops* (from Broom).
Fig. 121.—*Dipterus* (from Watson).

There is some variety in the bones of the skull roof anterior to the orbit. The prefrontal may be replaced by a process of the maxilla which extends upward behind the nasal to reach the frontal bone. In *Ichthyophis* this process is present as well as the prefrontal bone. *Ichthyophis* is also peculiar in having an adnasal between the nasal and the premaxilla and in the possession of a circum-orbital bone.

Whilst this skull roof presents a stegocephalian " completeness ", it is possibly only a parallelism, and comparable with the occasional complete roof found in certain genera of both Urodeles and Anura.

The stegocephalian similitude of the palatal aspect of the skull is due largely, if not entirely, to the double arch of teeth. These are situated, as to the external set, on the premaxilla and maxilla, and as to the internal set, on the prevomers and the palatine. This arrangement of the teeth is almost characteristic of the Labyrinthodont stegocephalians; it is found in Embolomerous, Rachitomous and Stereospondylous forms.

Not only is this so, but such an arrangement of the teeth in two complete arcades is not found elsewhere.

The Prevomers are large, resembling those bones in the Urodela.

The Palatine bones are extensive and form the anterior, lateral and posterior boundaries of the choanae. These apertures are placed relatively farther back than in either Anura or Urodela and are bounded medially by the prevomers.

An extensive palatine bone comparable with that of the Gymnophiones is found elsewhere amongst the amphibians only in certain of the Stegocephalia, e.g. *Eryops*, *Orthosaurus*, and *Capitosaurus*.

An Os Transversum has not been recognized in the palate of the Gymnophiones.

The so-called Pterygoid is a short, narrow, flat bone which extends from the pterygoid process of the quadrate to the posterior extremity of the palatine ; it lies in the floor of the temporal fossa, and forms the antero-median boundary to the via masticatoria. It is the homologue of the anterior arm only of the " pterygoid " of the Anura and the Urodela.

The quadrate is completely ossified and consists of a compact body which bears the articular surface on its lower face, and a glenoid cavity, on its posterior surface, into which the head of the stapes fits. Attached to the upper edge of the lateral surface of the body is a tympanic flange, of variable extent, which extends upwards, and both backwards and forwards, and sutures anteriorly with the lower edge of the squamosal bone. To the lower and inner corner of the body there is attached a tapering pterygoid process of variable length. The bone is attached by fibrous tissue only to the outer edge and upper surface of that part of the parasphenoid which extends laterally beyond the basis of the cavum cranii. The line of attachment extends from almost the postero-lateral corner of the parasphenoid to about the middle of the length of the orbit, and is along the medial surface of the body of the quadrate and the ventral surface of its pterygoid process. There is no trace of the basal and otic processes, nor of the ascending process. The ascending process was expected, for it is well developed in the chondrocranium of early embryonic stages.

The parachordal cartilages are to be seen imbedded in bone at the infero-lateral angle of the cavum cranii, but it is quite impossible in the youngest specimens at my disposal to find, in the transverse sections, any line of demarcation between the very extensive parasphenoid and the ectochondral bone which this encasement of the parachordals indicates must be present. Nor can one find, either in adult specimens of the prepared skull or in transverse sections, any indication of suture or duality of origin in the side walls of the cranium. These arise almost at right angles from the basis and are interrupted only by the vascular and nerve foramina. Immediately at the anterior boundary of the otic capsule, on the under surface of the floor of the cranial cavity, there is the carotid foramen ; this enters the cavum just behind the pituitary body, as determined by study of sections, there being no trace of pituitary fossa in the adult skull. Just as this canal reaches the cranial surface of the floor it gives off a branch which turns forward and laterad. The palatine branch of the facial nerve and the abducent nerve both enter this canal at the point of departure of the anterior branch, reaching this situation by passing caudad through a small canal which perforates the anterior margin of the prootic foramen. The fifth and seventh roots leave the cranial cavity together through the prootic foramen ; both their ganglion and that of the ophthalmicus profundus lie entirely external to the cranial wall in a recess which is bounded, as described by Norris and Hughes (1918), behind, by the body of the quadrate medially and posteriorly, and by the tympanic lamina of the bone laterally, with the prootic ossification above the ganglia. In front, the recess is bounded by the muscles of mastication, the parietal and prootic bone superiorly and the lateral flange of the parasphenoid and the pterygoid process of the pterygoid bone inferiorly. The various branches of the two nerves depart from this recess without any bony or cartilaginous structure intervening between them, excepting only the palatine whose course in this immediate neighbourhood has just been described.

In the sphenoid region my younger sections show the trabeculae and taenia marginata both encased in bone without sutures or other indication of any interruption in the ossification below the suture with the dermal roofing bones.

The Skull in the Stegocephalia.

(Figs. 119–124.)

The most completely known portion of the skulls of the Stegocephalia is the outer surface of the roof. The dermal bones are more numerous than in any of the recent groups. Besides parietals, frontals, prefrontals and nasals there are commonly present more or fewer of the following : post-parietals, tabulars, supratemporals, intertemporals, postfrontals, postorbitals and lachrymals as well as jugal, quadrato-jugal and squamosal bones.

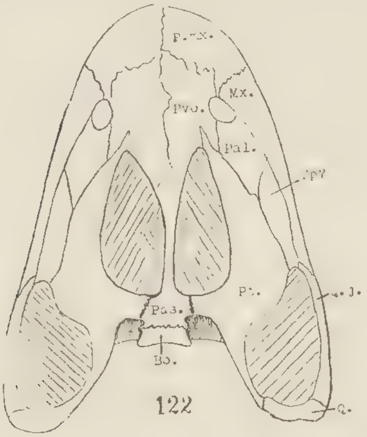
The general shape and position of these bones will be sufficiently gathered from the illustrations.

The illustration of the Dipnoan skull has been added for comparison. It is worthy of note that except for the fact that the parietal is undivided, this primitive amphibian presents all the bones of the dermal shield of the stegocephalian skull except the jugal and quadrato-jugal. Comparison with the dermal pattern of the embolomerous skull (p. 213) reveals an equally close resemblance.

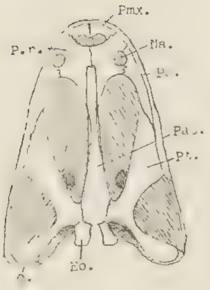
Maxilla and premaxilla are always present and well developed.

The ossification of the oto-occipital segment of the primordial cranium appears to have been as variable as in the Anura and Urodela combined.

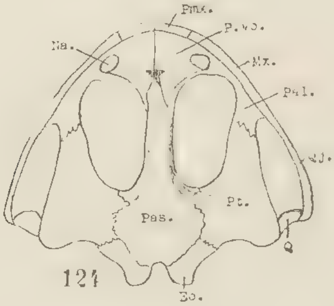
A separate " epipterygoid " bone has been described in isolated specimens of both rachitomous and stereospondylous skulls. It is, however, very probable that further investigation will show that the fragments so identified are but portions of the prootic ossification. There is little doubt that the epipterygoid bone of the reptiles is an ossification of the ascending process of the quadrate, and is essentially a reptilian feature. The complete absence of reptilian characters from the stegocephalian skull, and the retention of the ascending process in its primitive form in all the recent amphibians, renders it highly improbable that the bone should have been present in members of a group which must have been ancestral to the recent forms.



122



123



124

Fig. 122.—*Eryops* (from Broom). Tp. Os transversum.

Fig. 123.—*Cyclotosaurus* (from Fraas, after Goodrich).

Fig. 124.—*Batrachosuchus* (from Watson).

The ventral surfaces of three typical stegocephalian skulls are illustrated here, and from them a general idea of the relation and extent of the bones will be gathered.

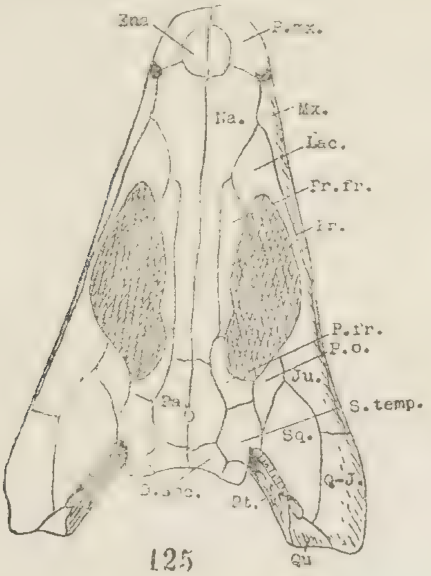
It remains to remark that the quadrate ramus of the pterygoid bone, in a number of genera, is folded around the posterior surface of the quadrate, rising towards the skull roof, and, apparently, contributing to the posterior wall of part of the tympanic recess. This dorsal extension of the pterygoid bone never rises so high as in the Embolomeri, and Cotylosaurian reptiles.

3. The Skull in the Embolomeri.

(Figs. 125–129.)

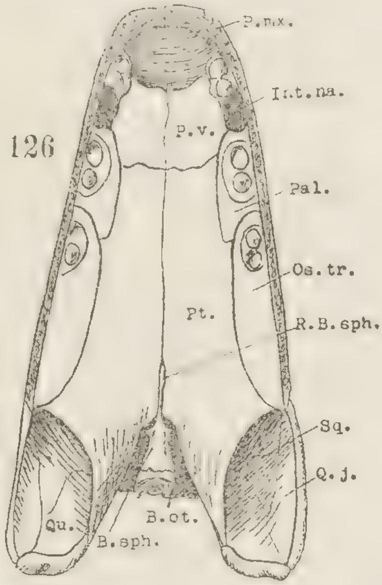
The following description is taken from Watson (1926). I have, however, been unable to accept the whole of his identifications of the bones he describes.

In its general facies this skull is essentially reptilian, the neurocranium is tropibasic, and, as in the reptiles, there results a compact cavum cranii with a narrower sphenoidal cavity lifted on to the dorsal edge of an interorbital septum. That essentially amphibian bone the large, primitive, synpterygoid, is not present on the base of this skull. The two most outstanding of the characteristics of the amphibian skull are therefore missing from this, and in their place reptilian characteristics are found.

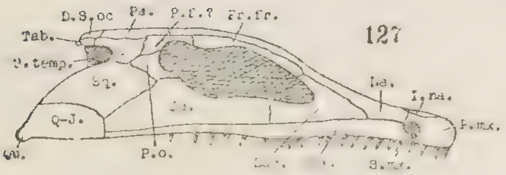


125

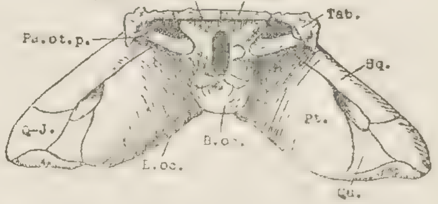
126



127



128



Figs. 125-128.—*Orthosaurus* (from Watson, 1926). Pa.ot.p., Parotic process.

The oto-occipital portion of the neural cranium is laterally compressed, and is provided on each side with a parotic process of typically reptilian form. Entering into the composition of this part of the cranium there are distinct exoccipitals, basi-occipital, supraoccipital, basisphenoidal, and prootic ossifications. Watson claims to be able to distinguish between the basi-sphenoid and a covering parasphenoidal ossification by slight differences in their texture in *Palaeogyrinus*, but says the bones are indistinguishable in *Orthosaurus*. He describes the " parasphenoid " as covering " the greater part of the lower surface of the basi-occipital, overlapping the sides of that bone nearly to its articulation with the otic bones ". He continues, " In front of the otic region the joint bone bears a pair of well formed basi-pterygoid processes which project laterally and somewhat downwards. The lower surface of each process at its root has a groove passing from the posterior round on to the anterior surface ; this housed the internal carotid artery."

There is some confusion here. Watson depicts, in *Palaeogyrinus*, a well marked suture between the basi-occipital and the bone in front of it on the base of the cranium. This suture meets the exoccipital above, so that the basi-occipital does not reach the prootic bone. Apparently it is the basisphenoid which the parasphenoid is believed to overlap.

In view of the other striking reptilian features, it is not advisable to accept the slender evidence of "slight differences in texture", as conclusive evidence that there is any membrane-derived bone covering the inferior surface of the basisphenoid. It appears more probable that the bone is a typical reptilian basisphenoid.

The groove on the inferior surface of the basitrabecular* process probably did not house the internal carotid artery. That vessel runs dorsally to the basitrabecular process in the reptiles, and dorsally to the plane of the parasphenoid bone in the Amphibia.

Anterior to the oto-occipital segment of the neuro-cranium there is an ossified interorbital septum which has been designated "sphenethmoid". The sphenoidal cavity is an excavation along the thickened dorsal part of this septum. The two olfactory canals leave the fore-end of the cavity, and tunnel the portion of the bone in front. Posteriorly the sphenethmoid articulates with the anterior end of the roof of the neuro-cranium behind the posterior end of the sphenoidal cavity. Below this articulation the posterior margin of the bone bears, about the middle of its depth, two processes which suture with the prootic. Below this again, the posterior edge meets the anterior end of the rostrum basisphenoidei and in front of this its ventral edge bears the splint-like "parasphenoid",† so characteristic of many reptiles. Two apertures are present between the posterior end of the sphenethmoid and the neuro-cranium. The upper of these was believed by Watson to have transmitted the Vth nerve only, the lower to have transmitted the optic and eye-muscle nerves and the internal carotid artery.

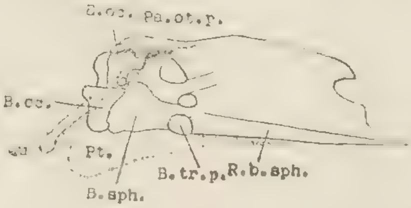


Fig. 129.—*Palaeogyrinus* (from Watson, 1926, but with the quadrate and pterygoid bones "restored" in dotted lines).

In view of the fact that it is quite unusual in the amphibians and the reptiles for the incisura prootica to be separated from the sphenoptic fissure by any cranio-mural ossification, it is more probable that the upper aperture transmitted all the nerves anterior to the VIIIth, except the olfactory, and the ophthalmic vessels, whilst the lower will have been the foramen of entry of the cerebral branch of the internal carotid artery.

So far as may be decided from Watson's figures and description, the pituitary fossa was situated immediately above and behind the planes of the basitrabecular process, and it would appear that the anterior part of the cavum cranii was sharply tilted upward immediately in front of the fossa. The floor apparently rose on the sloping posterior face of the sphenethmoid, between the two processes which separate the arterial from the other foramen, to reach the sphenoidal cavity, formed in the posterior end of the thickened dorsal part of the sphenethmoid bone.

The dermal roofing pattern is relatively simple, as compared with that of other labyrinthodont amphibian skulls, though more complex and primitive than that of any recent amphibian.

---

* The designation "basitrabecular", which Goodrich wisely adopts for the basipterygoid process, will be used instead of the older name. This course appears advisable because there is a distinct tendency on the part of a number of morphologists to disregard the fact that the process is an ossification of a process of the trabecula related to the fenestra hypophysios. In the result these careless thinkers find a "basipterygoid" developed as a process of the parasphenoid or situated far from the fenestra. The term basitrabecular should act as a corrective. One of the most surprising instances of disregard of the site of the trabecular origin of the basitrabecular process is the identification of the process in *Eusthenopteron* by Watson (1926). Clearly, if the bone identified as the basisphenoid is an endochondral ossification of the basi-trabecular plate it can be none other than a presphenoidal ossification; it is obviously too far forward to be regarded as a basisphenoidal ossification.

† It has recently been demonstrated that this "parasphenoidal splint" is an endoperichondral ossification and a presphenoidal not parasphenoidal bone (Kesteven, 1940*b*, 1941*a*).

In the mid-line the parietals cover the greater part of the oto-occipital segment of the cranium and extend forward over the posterior end of the sphenoidal cavity. Their common suture is interrupted by a pineal foramen. Behind the parietals a pair of dermo-supraoccipital bones are present. In front of the parietals the frontals may or may not be fused with the nasals, and in front of the last a pair of internasal ossicles may or may not be present. Tabular, supratemporal, postfrontal and prefrontal bones are present. In front of the prefrontal a typical reptilian " lachrymal " bounds the orbit anteriorly and extends, in some forms, right forward to the external nares, as in primitive reptiles. A postorbital bounds the orbit posteriorly. The squamosal makes sutural contact with the supratemporal, postorbital, quadrato-jugal, quadrate and pterygoid bones. The premaxilla sutures with the maxilla at the transverse plane of the external nares, and the latter bone extends back well behind the orbit, from which it is separated by the jugal.

The palate of the Embolomeri is, perhaps, the most characteristic feature of the skull, and is very dissimilar to that of any other amphibian.

The synpterygoid (parasphenoid or vomer) is reduced to a narrow splint lying along the ventral edge of the interorbital septum.

The pterygoid bones are very extensive and contribute the greater part of the bony palate. They meet in a common median suture which extends from that between the prevomers back almost to the posterior end of the palate. The parasphenoid appears between them posteriorly. Laterally they suture with the palatine and os transversum. There is no suborbital or subtemporal deficiency in the palate. At the transverse plane of the anterior margin of the via masticatoria, the lateral margin of the pterygoid swings mediad and caudad, forming the whole of the median boundary of the " via ". Also, at this transverse level, the inner portion of each pterygoid turns dorsad, rising in close relation to the side wall of the auditory capsule, apparently in the manner indicated by the dotted line in Fig. 129, till it meets the inner margin of the squamosal just behind its suture with the supratemporal. The inner margin of the pterygoid, here better termed its dorsal margin, now continues caudad in sutural contact with the postero-medial margin of the squamosal till the tympanic notch is reached. The posterior limit of the bone is indicated in Fig. 127, where it was shown as it lies in contact with the inner and posterior surface of the quadrate just proximal to the articular surface.

The os transversum, palatine, and prevomer are simple bones whose form and relations are sufficiently indicated in the figure of the palatal aspect of the skull.

The quadrate is largely encased by the quadrato-jugal, squamosal and pterygoid bones, but is exposed in the roof of the via masticatoria, and probably articulated with the lateral end of the parotic process as in many reptiles.

In the extended description of the Embolomeri which Watson gave in the Croonian lecture (1926) he fails altogether to describe the relation of the quadrate to the skull. In an earlier paper (1913) he describes the quadrate as being exposed on its under surface and as " passing upward on the under surface of the roof of the skull until it is received into a slit in the squamosal, which thus covers it both dorsally and ventrally ".

On a later page he wrote, " Examination of these primitive and extremely well preserved skulls seems to show that the ordinary idea of the autostylism of the tetrapoda is incorrect in postulating a connection between the pterygo-quadrate cartilage and the otic region. It is, I think, quite certain that there never was such a connection in primitive forms, except through the dermal bones of the temporal region."

Although not so stated, it would appear that his later examination of embolomerous material has caused him to regard the above description as incorrect. The squamosal of *Palaeogyrinus* is described as terminating behind " by overlapping the dorsal surface of the quadrate ". Apparently, then, there is no support at all for the suggestions relative to the autostylism of the Tetrapoda.

The epipterygoid has been identified in *Palaeogyrinus*. It is a short ossicle which, lying against the anterior edge of the ascending posterior lamina of the pterygoid, articulated below with the basitrabecular process and had an expanded free upper extremity.

The tympanic notch mentioned above is a pit situated on the postero-dorsal surface of the quadrate and under cover of the squamosal laterally and the upper margin of the ascending lamina of the pterygoid medially. Watson writes of the notch, " There is, in all the members of that group of Embolomeri which includes *Loxomma*, a curious pit on the quadrate, so placed that it faces toward the otic capsule, which must have lodged some structure. This can only have been a process from the cartilaginous stapes, representing the lower part of the hyomandibular ".

The tympanic cavity in both amphibians and reptiles lies behind the quadrate and below the parotic process. In the embolomerous amphibians, the remarkable ascending lamina of the pterygoid has obviously walled in the tympanic space between itself and the quadrate, whilst the squamosal completes the walling-in dorsally. Only the distal aperture of the cavity remains. This is the tympanic notch.

Watson has designated a certain pit on the outer wall of the otic region the " pseudo-fenestra ovalis ", and he rightly says that the pit, in *Palaeogyrinus*, is situated in the position that the fenestra ovalis might have been expected to occupy. The situation of the pit in *Eogyrinus*, in front of the parotic process, is, however, not one in which the fenestra ovalis would be sought. It is probable that when material has been found which exhibits the true relation of the head of the quadrate to the skull, the fenestrae of the ear will also be located.

APPENDIX.

The " Sauramphibia ".

It has been claimed that the Embolomeri are the most primitive amphibians known, " and those which most nearly resemble the fish ancestors of that class " (Watson, 1926).

To the present writer this appears to be an untenable position, and to rest very largely upon a fundamentally wrong concept.

It is quite apparent that the view can only be based on the assumption that the primitive pterygoids were large expanded bones meeting, or nearly meeting, in the mid-line of the palate, and that the primitive " parasphenoid " was a narrow splint.

It is believed, here, that it is not possible to place any but quite secondary values upon the similarity or dissimilarity of dermal roof patterns, as evidence of phyletic relationships.* It is so readily demonstrable that closely allied forms in most, if not all, vertebrate groups have, at times, very dissimilar roof patterns, whilst widely unrelated forms in different groups may present essentially, and even actually, similar roof patterns.

It is therefore, to the more stable endochondral ossifications and the bones of the palate that one must turn for reliable evidence in phylogenetic question.

Goodrich (1930, p. 318) accepts Watson's view and states the position relative to the history of the parasphenoid more explicitly : " The parasphenoid in the Embolomeri was comparatively small, closely connected with the basisphenoid posteriorly, and extending forward below the sphenethmoid as a narrow grooved blade. In the more advanced types (Rhachitomi, Stereospondyli) the interpterygoid palatal vacuities become progressively enlarged, the parasphenoid expands behind and becomes immovably sutured to the pterygoid."

The discussion of this question may well be introduced by a brief statement of facts of particular relevance :

(1) The basisphenoid bone is an endochondral ossification of the primordial chondrocranium in the region of the hypophysis cerebri, and is either perforated by the hypophysial fenestra or forms the floor of the pituitary fossa, and is usually perforated by the canal for the internal cerebral branch of the internal carotid artery.

(2) It is therefore possible to recognize a basisphenoidal segment of the basis cranii, and in the Amniota this segment lies immediately in front of the basioccipital segment ; its position is determined by that of the hypophysis cerebri in all vertebrates.

(3) In the Anamniota as a group, the basisphenoidal segment of the cranial floor is either (*a*) not ossified at all, (*b*) incompletely ossified, or (*c*) ossified in complete continuity with the ossification of the occipital segment and the auditory capsule.

(*a*) Not Ossified at all.—Omitting the typical Elasmobranchii, which, in the complete absence of ossification, shed no light on the present question, this condition is found in a majority of the Chondrostei, Urodela and Anura, and in all the Dipnoi. There was also complete absence of ossification of the basisphenoidal, pituitary region in the Osteolepida.

(*b*) Incompletely Ossified.—This condition is characteristic of the whole of the bony fishes excepting only those mentioned above. In fishes with a myodome, the little bone which has been identified as the basisphenoid lies entirely in front of the pituitary body and, on that account, its homology with the basisphenoid of the Tetrapoda has been questioned and it has been proposed to designate it "suprasphenoid". On the other hand, the horizontal transverse arm of the bone in such fishes certainly occupies the position of the anterior portion of the pituitary fossa, and that is basisphenoidal in the Tetrapoda. It would seem that it is certainly homologous with, at least, the anterior portion of the bone. In this respect the Palaeoniscid skull resembles the majority of the bony fishes. In the absence of the myodome the basisphenoid, if present at all, is exceedingly thin and is so intimately fused with the underlying "parasphenoid" that it is quite impossible, in adult skulls at least, to recognize the composite nature of the bone.

---

* It has, however, already been noted that there is nothing in the dermal roof pattern of early Dipnoans to contra-indicate community of origin of Dipnoans, Embolomeri and Euamphibia.

In the apode amphibians it is questionable whether any basisphenoidal ossification is present at all. In none of the adult or young specimens examined, in serial sections, is there any indication of a dual contribution to the bony floor of the pituitary region. Apparently a very extensive basicranial fontanelle is floored by the synpterygoid only, though there may be a small contributing basisphenoidal element completely fused with it, as in the fishes without a myodome.

(c) Ossified in complete continuity with the occipital segment and auditory capsule.—This condition is found in some of those amphibians in which the cartilaginous chondrocranium is extensive in this region. Endochondral ossification commences in definite occipital and auditory centres and extends uninterruptedly forward along both the floor and sidewalls of the cavum cranii, and ultimately a continuous bony case results, in which no sutures are visible.

(4) In the Anamniota the synpterygoid is an extensive bone on the basis cranii. It commences at, or behind, the occipital segment and, extending forward beneath the pituitary, sphenoid and (in some forms) ethmoid regions, supplies the strength which the absence of endochondral ossifications calls for. In both the fishes and the amphibians this bone is characteristically expanded below the auditory capsules and, when the skull is laterally compressed in the auditory region, this lateral auditory wing of the bone rises on the lateral wall of the capsule.

(5) In the Amniota the "parasphenoid" takes the form of a narrow splint applied to the lower surface of the rostrum basisphenoidei and the membranous cartilaginous or bony interorbital septum, and is really a presphenoid ossification, not a membrane bone.

(6) Excepting only in the Dipnoi, in the presence of a well, or moderately well, developed parasphenoid, the pterygoid bones never meet at the mid-line. It is only when the "parasphenoid" takes the form of a prepituitary splint, which we now identify as the vomer, that the pterygoids meet one another medially.

(7) The divergent pterygoids are characteristic of the Anamniota, the convergent of the Amniota.

Features such as these, which may be described as being characteristic of the whole of the Anamniota, must assuredly be regarded as having resulted from a community of inheritance.

The Anamniota are undoubtedly more primitive than the Amniota, and the Fishes than the Amphibians.

Therefore features characteristic of the Anamniota must be regarded as more primitive than those characteristic of the Amniota.

The unossified or poorly ossified pituitary region of the basis cranii, strengthened and supported by an extensive parasphenoid which had also lateral auditory wings, is to be regarded as being more primitive than a well-ossified basisphenoid bone and a parasphenoid reduced to the vomerine splint.

The separated and divergent pterygoids are to be regarded as being more primitive than the contiguous convergent pterygoids.

It follows that Amphibians of the type of the Rhachitomi, Stereospondyli, the Anura, Urodela and Apoda, which possess these primitive features, must be regarded as being more primitive than the Embolomeri, and this would still hold good even were there no representatives of those (regarded as the more primitive) of equal geological antiquity with the others.

On the other hand, there can be no doubt whatever that the Embolomeri are so essentially reptilian in their cranial characters that they may be regarded as the most advanced of all the amphibians, "advanced" being taken to mean more nearly like to a group of vertebrates which we are all agreed to regard as standing higher in the evolutionary scale than the amphibians.

Comparison of the embolomerous skulls with those of the anapsid cotylosaurian reptile, *Seymouria*, and its allies will discover for the investigator that, bone for bone, and area for area, there is a similarity so complete that one is forced to inquire further in order to satisfy oneself that the one is an amphibian and the other a reptile.

Since it is beyond question that the features wherein the Embolomeri differ from the remainder of the Amphibia are essentially reptilian, it follows that such resemblances as they present to the fishes must be either only apparent, due to wrong interpretation of the component structures in the crushed and distorted skulls, or due to inheritance from some common ancestor of all.

When it is remembered that the Cotylosauria date right back to middle Carboniferous times it becomes clear that, already, that advance in structure which was to give rise to the reptiles must have taken place in early Carboniferous times. It would appear that once the tetrapod structure had been evolved, the early members of the group were exceedingly plastic and that differentiation into the various divisions took place very rapidly. The result of this rapid differentiation was that, side by side, chronologically, we find the fishes, dipnoans, amphibians and reptiles, and between these last two the embolomerous amphibians, which alone of their class may be regarded as having stood in the direct current of evolution which produced the reptiles and Amniota generally. The rest of the Amphibia are, therefore, to be regarded as constituting a specialized end-group, or a branch on the genealogical tree of the animal kingdom.

Since the parasphenoid of all the fishes, with the possible, but improbable, exception of certain of the Osteolepida, was an expanded bone with lateral auditory wings, the view that would regard the primitive amphibians as having the vomerine type of parasphenoid and the later, more specialized forms, as having a parasphenoid which has become expanded as a result of, or as one of the features of, that specialization, surely runs contra to the circumstantial evidence available and to probability. The view necessarily assumes that the peculiar narrow parasphenoid of the osteolepid* fish was the primitive form of the bone and that the expanded form found in all other anamniotes, except the Embolomeri, was, and is, a modification of the unique forms. Since both are parasphenoid bones the inference that one is a modification of the other is inescapable.

If this be not the assumption on which the view is based, then another equally untenable position must be taken. It being granted that the, almost universal, expanded parasphenoid is the primitive, it is assumed that in the Osteolepida it has been reduced to the narrow vomerine type, and through them handed on to the primitive amphibians. At this point evolution has taken two divergent directions. On the one hand the reduced parasphenoid is retained, and the reptiles result; on the other the expanded primitive form is once more developed and the rest of the amphibia are evolved.

The position is untenable because it also involves an acceptance of a belief in the possibility of a reduction in the progress of endochondral ossification of the basis cranii, and a loss of the basisphenoid ossification which is so successfully achieved by the Embolomeri.

Actually the belief that the Embolomeri are the most primitive amphibians rests upon the further belief that in their cranial structure they resemble the Osteolepida, and that aspect of the question has already been dealt with.

The reptilian characters of the embolomerous palate will be discussed again in a later section; suffice it here to remark that they are very real and indicate a not distant alliance with the Reptiles. On this account it is now proposed that they be separated in our classification from the rest of the Amphibia under the significant title of "Sauramphibia".

THE PHYLOGENY OF THE AMPHIBIA.

1. General Considerations.

In his remarks on the affinities of the Arthrodires which form the concluding section of his work on the Head of the Macropetalichthyids, Stensio (1925) expresses the opinion that they are to be considered as an offshoot of the Elasmobranchian stem of fishes. The evidence which he advances in support of this view is as convincing as, in the nature of the problem, appears possible, and there will be few who will disagree with the conclusion he arrived at.

In the course of his discussion he points out that "close relationship between the Arthrodires and the Elasmobranchs of course implies either that bone has arisen independently in different groups of vertebrates or that it is a very old sort of tissue that was present already among the most primitive vertebrates and from these was bequeathed to the common ancestors of the Arthrodires and Elasmobranchs ".

---

* It should be remembered that the Osteolepida which present the peculiar narrow parasphenoid are known only from imperfect crushed specimens, so that it may be that the lateral wing has not been described because it has not yet been found, and not because it was not present in the complete skull.

In support of the second alternative he points out that in the earliest Holocephali known there were related to the cranium, bone-like, or perhaps true bony, plates. He also draws attention to the Cephalaspids, Ostracoderms and the Acanthodei, all provided with bony shields and plates, and remarks of *Menaspis*, one of the Cochliodontids, there is evidence of " armour on the head and anterior part of the trunk ".

Whilst it is a fact that the palaeozoic and early mesozoic Elasmobranchs were more generally equipped with bony head-plates or relatively large bony scales, and that this is definitely evidence of their derivation from an ancestor provided with bony shields, it is not evidence that the bony structures are more primitive than the cartilaginous basis on or in which these bony shields are developed, nor, indeed, is that implied by Stensio.

On the other hand, if there be truth in the suggestion that the common ancestor of the Arthrodires and Elasmobranchs was already provided with the power to develop bone, both endochondral or at least ectochondral, and membrane-derived, we may reasonably ascribe all these bony features, wherein the bony fishes and the Dipnoi resemble one another, to that common ancestor.

It is no longer necessary to postulate an ancestor common to these animals and not to the Elasmobranchs. In other words it becomes possible to visualize the separation of the three groups from the one stem.

It may be suggested that already amongst the palaeozoic fishes which, heretofore, we have agreed to regard as Elasmobranchs, it is possible to recognize the beginning of the three groups.

The Acanthodei may well be regarded as presenting an approximation to the primitive Teleostome, whilst the recent Chondrostei would be regarded as presenting a persistent and more advanced remnant of that group.

The Holocephali would be regarded as the most primitive form of the dipnoan stem, the modern representatives of the group being regarded as degenerates in relation to the formation of bone. A parallel case of degeneration in this respect is presented by the Acipenserids on the one hand and the Polyodontids on the other, amongst recent fishes.

Whilst their general morphology indicate that the Holocephali are unequivocably Elasmobranchs, it is still not without significance, especially in view of the geological antiquity of the group, that they possess a quadrato-maxillary arch which is firmly ankylosed to the cranium, for, otherwise, the existence of Elasmobranchs of great antiquity which had autostylic and monimostylic fixation of the arch, indicates that this modification of the manner of attachment of the upper jaw is of still greater antiquity and was initiated and brought almost to the dipno-amphibian condition amongst the elasmobranch fishes.

The concept that the Elasmobranchii, Teleostomi and Dipnoi all arose independently from a more primitive group, at about the same time, explains both the similarities and dissimilarities which these three present amongst themselves, and also their almost equal antiquity.

It may be remarked that not only these three groups but, maybe, also the Arthrodires, Anaspida, Antiarchi and Cephalaspids arose from the same primitive generalized vertebrate group. The Ostracoderms perhaps represent a more primitive form of fish than any of the rest.

The most significant features common to the Dipnoi and the Holocephali, and those which give rise to the suggestion that it is from a form similar to the latter that the former have been evolved, are those features of the muscular anatomy which have already been discussed in this connection, particularly the form of the muscles of mastication and the Csd.2 pars quadrato-hyoidea, and the autostylism of the maxillary arcade.

The fact that the Holocephali are archiprosencephalic, whilst the Dipnoi are neoprosencephalic is a complete barrier to any suggestion that the Dipnoi are directly descended from the Holocephali. It is, however, not without significance that those Elasmobranchs which are regarded as the most primitive of the recent forms, the Notidanidae and the Holocephali, have elongated and slender forebrains, which in their form and simplicity may well have been the " raw material " from which the neoprosencephalon was evolved.

Any dogmatic statement on the subject were little short of foolishness, for the whole subject is almost pure speculation, but it may be said that speculating on the interpretation of the very meagre evidence available leads one to the impression that the Dipnoi are descended from elasmobranchian ancestors which probably presented similarities, if they were not actually allied, to the Holocephali.

The evidence of the cephalic musculature and of the cranial structure, in its bearing on the " dipnoid " ancestry of the Amphibia has already been discussed.

In a recent communication on the problems of vertebrate morphology Professor Graham Kerr (1932, p. 420) writes, " It may be accepted as one of the canons of morphological science that the reliability of its conclusions bears a distinct relation to the breadth of their foundations. Conclusions as to the systematic position of particular vertebrates in the scheme of natural classification, and conclusions as to the evolutionary path along which their bodily structure has progressed towards its present-day condition, must, in order to be reliable, conform to the above mentioned canon. In particular it is essential that due regard be paid to all the available data whether these are provided by the anatomist, the palaeontologist or the embryologist . . . Conclusions resting on evidence provided by a single organ-system should be given only a cautious and provisional acceptance. And if that particular system be the skeletal—which in the case of extinct animals is as a rule alone available—the need for caution is greatly intensified."

Of the systematic position of the Dipnoi he writes (p. 421), " The study of Dipnoan structure during its various stages up to that of the adult leads to two certain conclusions : (1) that the existing Dipnoi constitute a self-contained group quite independent of the Teleostomi, and (2) that the closest affinities of the Dipnoi are with the Amphibia."

This statement is followed by a long list of the evidence on which the conclusions are based.

The present writer had previously (1931) reviewed as completely as was then possible to him those features of the development and adult anatomy of the Dipnoi and Amphibia which yielded evidence of the close affinity of the two groups. The conclusion then arrived at has been further confirmed by the work done on the development and adult condition of the musculature. For that reason the Dipnoi are here treated as primitive amphibians.

In order that this conclusion may have that breadth of foundation which Kerr very justly demands for such, I quote the list he gives and refer to my own list and comments of 1931.

Kerr (1932, p. 421) wrote, " As regards general form of body a young Lepidosiren presents all the general appearance of a Urodele, even showing a slight narrowing of the neck region, practically the only conspicuous distinguishing feature being the limbs, although in the case of Lepidosiren this has become less marked owing to the limb having lost its paddle form and assumed, or, as I would say, reverted to a styliform condition, differing from a pentadactyle limb mainly in the absence of a terminal expansion to form a foot and the absence of concentration of flexibility into localised joints. The lung of the young Dipnoan, with its ventrally placed glottis, the protostylic attachment of the lower jaw to the cranium, the presence of an atrial septum, the tendency of the pocket valves of the conus to revert to the condition of continuous endocardiac ridges, the splitting of the ventral aorta by a horizontal septum into pulmonary and systemic cavities, the presence of a posterior vena cava, the high development of the pallium of the cerebral hemisphere with its incipient cortex, the presence of choanae opening into the buccal cavity, the development of outgrowths from the endolymphatic duct of the otocyst, the development of the external gills agreeing exactly with those of the urodeles, in the larvae of two out of the three genera, and the fact that the cement organs where they are present arise from the ectoderm without any participation by the endoderm, constitute together an assemblage of features which demonstrates irrefutably the close relationship with and the distinctness from the other fishes. There is another feature which would be by itself almost convincing to anyone experienced in Dipnoan study, namely the general agreement in histological structure of the tissues with those of the Urodele Amphibia."

Kesteven wrote (1931, pp. 183–196) :

" There are a large number of characters wherein the dipnoans resemble the amphibians more than other fishes do, and, though the contrary has been argued, not one of them is devoid of phylogenetic significance. I give a list of the characters in question and discuss the more important of them.

Adult Features.

The mode of swimming.
Autostylic and monimostylic suspension of the maxillo-mandibular arch.
The fenestration of the nasal roof.
The homology of the supra-orbital bone with the amphibian prefrontal.

The form of the brain
The possession of internal nares.
The division of the auricle into right and left halves.
Certain features of the arterial system.
Certain features of the venous system.
The possession of true external gills.
The form of the air-bladder and its function.
The structure and position of the glottis.
The possession of an epiglottis.
The possession of a true pelvic girdle.
The mating call.

Embryological and Larval Characters.

The general course of the development.
The development of the external form.
The mode of development of the two-chambered auricle.
The origin of the amphibian characters in the arterial system.
The origin of the amphibian characters in the venous system.
The mode of origin of the cerebral hemispheres.
The early form of the chondrocranium.
The development of the buccal cavity.
The form of the pituitary involution.
The development of the flask glands.
The development of the cement organs.
The history of the palato-quadrate.
The history of certain cranial myotomes and their derived muscles.

"*The mode of swimming.*—' When we consider the *clumsy movements* of the only existing fish retaining this type of fin (*Ceratodus*) . . . ' (Kerr). This is the only reference I can find in literature to the peculiarity of the mode of progression of *Neoceratodus* through the water. Whereas the great majority of fish appear to strike the water with the tail, a few of weak muscular development in the caudal region, and practically all fish when sick and exhausted, appear to undulate through the water much as a snake travels over the ground. In these cases the body flexures are, so far as my observations serve me, but two in number, producing a very wide open S-curve. Now the swimming motions of *Neoceratodus* recall these undulations ; there is a complete absence of the tail ' stroke ', but more than that, the undulations follow one another so that there appears to be a sequence of them, and they recall in a most striking manner the wagging of the ' tadpole's ' tail.

" It is a fact not without significance that this is the mode of swimming of practically all fish larvae. Again I speak from personal observation, for I can find nothing in literature on the matter. The opportunities of a single individual for making such observations are of necessity limited as to the variety of forms observed. The youngest pelagic fish larvae ' wiggle ' through the water ; as they increase in size the number of flexures of the body become less. Growing a little older, the youngster will, when frightened, start off with a jump, wiggle rapidly for a little space and then seem to be propelled through the water with the body held rigid ; closer observation discovers the tail striking the water with a lateral and oblique stroke. The adult starts off with a similar jump, the result of a powerful lateral sweep of the tail, and then continues with a rigid body.

" Since it is characteristic of larval forms, ' wiggling ' or undulatory progression may be regarded as having been the primitive mode of swimming, and there is ample confirmation of this inference in the metameric arrangement of the longitudinal musculature. The interest of these phenomena to our present problem lies in the fact that alone among the compact vertebrata, the adult dipnoans and the amphibians retain an archaic mode of swimming. Is this evidence that in their common ancestry there was none which had developed the tail as *the* organ of swimming ?

" *The autostylic and monimostylic suspension of the maxillo-mandibular arch.*—The mode of attachment of the quadrate to the neurocranium in the dipnoans is essentially and in *Neoceratodus* identically the same as in the amphibians, excepting only the aberrant *Ichthyophis* and *Siphonops*.

Herein the lung-fishes differ, it may be said, fundamentally from the rest of the fishes and resemble the frogs. As this matter will be returned to in the next section it may be left for fuller discussion there.

"*The fenestration of the nasal roof.*—The similarity noted here and the fact that it did not extend to other fish was noted by Bridge. Having described the fenestration, in a footnote he remarks : 'With the exception of the Dipnoi, this curious fenestration of the nasal roof occurs in no other vertebrates except certain Urodele Amphibia, and affords another instance of the many homoplastic modifications which are to be noted in the two groups.' It is a fact that, as he further notes, this fenestration has been observed, but hardly more than indicated, in certain selachians.

"Like several of the other features, which are here passed in review, wherein the lung-fishes resemble the amphibians more than any other of the fishes, this is not advanced as being in itself of phylogenetic significance, but considered in conjunction with all the others it lends weight, and receives weight. It is certainly significant that so 'many homoplastic modifications' are found in the Dipnoi, whilst none are found in the ganoids which lived side by side with them. Why, one cannot but ask, are the resemblances between the crossopterygians and amphibians regarded as of phylogenetic import, while those between Dipnoi and amphibians must be deemed merely homoplastic ?

"*The homology of the supra-orbital bone with the amphibian prefrontal.*—This is a homology maintained by Bridge, but Kesteven has maintained the homology of the teleostean ectethmoid and the amphibian prefrontal ; if he be correct, this feature is not a peculiarity of the dipnoans.

"*The form of the brain.*—Herein we have a feature which is unquestionably of phylogenetic import. Here, in the Dipnoi, we have the inception of those modifications of the cerebral hemispheres which culminate in the mammalian neopallium. It is quite beyond question that, whereas there is a fundamental similarity in the brains of all other fishes, there is an equally fundamental departure from that type in the dipnoan brain, and that we must turn to the amphibians for a similar brain, and, further, that having so turned, we find the similarity between dipnoan and amphibian brains as complete as that between the rest of the fishes among themselves.

"*The possession of internal nares* may be merely a homoplastic variation, but equally it may have been derived from an ancestor common to the gnathostomes possessing them. As far as my reading serves me, it would appear that the dipnoi are the only animals below the Amphibia so endowed.

"*The division of the auricle into right and left halves.*—That this does not occur in other fish is, of course, not in need of telling, but, together with the form of the lung and the related modifications of the arterial and venous systems, it has been regarded as the result of parallel modification under the drive of similar environment. On the other hand, it is equally well known that in certain of the ganoids, especially *Polpyterus*, the air-bladder acts as a subsidiary respiratory organ (Budgett). There is not wanting evidence that in the Teleostei also the air-bladder acts as a subsidiary respiratory organ (Jobert). Although this is so, it is also a fact that in neither *Amia, Lepidosteus, Polypterus* nor the teleosts investigated by Jobert is there any indication of those modifications of the heart and vascular system which, in the dipnoans, resemble the amphibian arrangement. We have here, then, circumstantial evidence that there was nothing in the mere assumption of a respiratory function by the air-bladder to condition variations in the vascular system after the amphibian pattern ; some other circumstance or factor must be invoked. Since it *did* work in the same manner on both dipnoans and amphibians, it is at least not unreasonable to postulate 'inherited potential'.

"*The arterial system.*—Bridge briefly reviews the arterial systems of the dipnoans as follows : 'As in so many other features of its anatomy, *Neoceratodus* exhibits in its arterial system abundant evidence of the widespreading affinities of the group to which it belongs. In its branchial arterial system *Neoceratodus* presents a singular combination of features which, individually, are characteristic of Amphibia and Elasmobranchs. Special amphibian features may be noted in the origin of the afferent branchial arteries almost simultaneously from the anterior end of the conus arteriosus ; in the origin of a lingual artery from the efferent vessel of the first arch ; and in the derivation on either side of a pulmonary artery from the fourth epibranchial artery. Agreement with Elasmobranchs is to be found in the presence of two efferent branchial vessels in each branchial arch, although the relations of these vessels are more primitive than in most adult Elasmobranchs, inasmuch as the two efferent vessels of the *same* arch unite to form an epibranchial artery ; and also in the origin and distribution of the anterior and posterior carotids. Lastly may be mentioned the fact that *Neoceratodus* agrees not only with the Amphibia, but also with those generalized Teleostomi, *Polypterus* and *Amia*, in the mode of origin of the great arteries for the air-bladder ' (from the fourth pair of efferent branchial vessels). This last is described as a ' significant resemblance ' (p. 338).

" ' Of the two remaining Dipnoi, the arterial system of *Protopterus* is better known than that of *Lepidosiren*, but in both cases further research is needed before a satisfactory comparison can be made with *Neoceratodus* and other Vertebrates. It is evident, nevertheless, that both genera differ from *Neoceratodus* in approximating more closely to the Amphibia than the lower fishes, in so far as the branchial part of the arterial system is concerned.' [*Lepidosteus* in its arterial system is said to offer ' a singularly interesting transition from the Elasmobranch to the Teleost ' (*l.c.*, p. 334).]

" In this comparative review Bridge was struck by the dual nature of the similitudes of the arterial system, those wherein it resembled the amphibian on the one hand and those wherein it resembled the elasmobranch on the other ; characters new and characters archaic.

" Of the new characters, conceivably, the origin of pulmonary arteries from the fourth pair of efferent branchial vessels may be causally ' post hoc ' to the assumption of respiratory function by the air-bladder, but not so the peculiar origin of the lingual artery or the bunching together of the afferent branchial vessels at the anterior end of the conus arteriosus ; else why has it not happened in *Polypterus* and *Amia* ? In both of these the air-bladder functions as a respiratory organ supplied by pulmonary arteries similar to those of *Neoceratodus*.

" *The venous system.*—Features of this system which may be regarded as pointing to a common ancestor for the dipnoans and the Amphibia are the renal-portal vein, the inferior vena cava and the anterior abdominal vein. Bridge writes : ' Less is known of the venous system of *Protopterus* [than of that of *Neoceratodus*], but it is certain, nevertheless, that it presents a more advanced grade of evolution . . ., and, except for the doubt as to the existence of the anterior abdominal vein, it is essentially similar to that of a Urodele Amphibian in which the right posterior cardinal vein has aborted.' There is no evidence that any of these features is merely a homoplastic variation.

" *The external gills.*—Herein the Dipnoi share a distinction with the Crossopterygii as well as the Amphibia, and we are to assume that the feature was present in their common ancestor, but it is not evidence that the ancestor in question was more crossopterygian than dipnoan in character.

" *The form of the air-bladder and its function.*—Although the air-bladder of *Polypterus* is more complex than that of other ganoids, and to that extent it stands as an intermediate stage between the dipnoans and other fishes, it is not of great phylogenetic significance because it has not associated with it those other modifications of the respiratory and vascular systems which in their totality bring about the striking resemblance between the dipnoans and the amphibians. In the case of *Polypterus* the increase in the complexity of the walls of the air-bladder is a single isolated modification, and, moreover, one that may with justice be regarded as resulting from the influence of the environment ; although the resemblance is marked, it well may be an analogous modification and not a homologous one. The development of a glottis might also be regarded as but another part of the same modification. On the other hand, the ventral position of the glottis cannot be so regarded ; there are forms with air-bladder almost as complex and a dorsal glottis. It is believed that this position of the glottis is evidence of the existence of closer relationship between the Crossopterygii and the dipnoans than between the former and other ganoids. There is other evidence in support of this belief.

" *The possession of a fibro-cartilaginous epiglottis* by two of the dipnoans is not, in itself, significant, but being superadded to the glottis it is ; unless we assume that it was evolved *pari passu* with the glottis, it surely pushes the origin of the glottis further back in time. Does it not indicate that the respiratory function of the air-bladder in the dipnoan ancestry was so well established that already there was diversity in the superadded structure amongst the members of the group ?

" *The mating call* of *Neoceratodus* is essentially similar to that of the frogs. I know of no fish with a mating call.

" *The development of the cerebral hemispheres.*—Kerr (1902), when describing the development of the brain of *Lepidosiren*, describes the hemispheres as arising as ' two separate lateral bulgings of the wall of the thalamencephalon ' and notes that herein the development of the brain of

Lepidosiren presents features of fundamental importance to a proper understanding of the morphology of the vertebrate brain generally. Professor Kerr returns to this question in his account of the development of *Polypterus* (1907), and his remarks are worthy of quotation in full.

" 'As has been pointed out elsewhere, I hold the view of von Baer, Reichert, Goette and Studnička that the true cerebral hemispheres *as seen in Vertebrata from Dipnoi upwards*, are to be looked upon as primitively paired structures—as lateral evaginations of the wall of the primitive fore-brain, developed doubtless in order to give space for the great increase in the mass of nerve matter in this region correlated with the increasing development of the olfactory organ. I find it difficult to realize how anyone can fail to be convinced that this is the correct view to take of the morphology of the hemispheres, *looking at their mode of development in the Dipnoi and Amphibia* and to their adult relations in the higher forms where that potent disturbing factor—the yolk sac—is present. In *Polypterus* a quite similar increase takes place in the mass of nervous matter forming the sides of the primitive fore-brain, but in this case there is no evagination of the brain wall to form hemispheres, beyond the small pair of olfactory lobes. Room is found for the nervous mass in other ways: (1) the side wall becomes greatly thickened to form the so-called "basal ganglia"; (2) the thalamencephalon increases much in length and (3) the thickened portion becomes slightly invaginated instead of being evaginated. The nervous material which corresponds with the whole of the hemisphere in the higher forms—including the pallium or mantle—lies in the thickened wall of the thalamencephalon. What is ordinarily termed the pallium in the Crossopterygians is nothing more nor less than the roof of the thalamencephalon, which is of course epithelial here as elsewhere. The conditions in Actinopterygian Ganoids and Teleosts are obviously similar to those in *Polypterus*: what is ordinarily called the pallium in these forms is simply the epithelial roof of the primitive fore-brain, while the so-called basal ganglia are thickened walls including what corresponds to the whole of the hemispheres in higher forms.' Kerr concludes by pointing out that Studnička has already given utterance to exactly the same views'.

" Clearly we are compelled to conclude that the form and mode of development of the cerebral hemispheres are features wherein the Dipnoi differ fundamentally from the fishes and resemble the amphibians.

" Gregory finds that the Dipnoi and Crossopterygii were derived from a common ancestor, and concludes his paragraph thus: 'Nor should the difference in brain structure of these modern forms outweigh the abovementioned resemblance, for there is no evidence that the brains of the Devonian Crossopterygii were any more divergent from each other than were the other parts of the body.'

" With this conclusion I am unable to agree. If our knowledge of the recent dipnoans were confined to fossil skeletal structures only, we would unhesitatingly classify them along with the rest of the dipnoans, and we should find that they all differed from the crossopterygians in one fundamental respect—they are autostylic, while the Crossopterygii are without exception neohyostylic. In the very nature of the problem we can have no direct evidence as to the form of the Devonian brains, but it is surely more likely that the Devonian dipnoans resembled the recent in this respect, having inherited this brain form from an earlier ancestor, from whom also the Amphibia inherited it. If this view be not accepted, we must accept one of two alternatives: (1) the dipnoans and amphibians independently developed this type of brain; (2) this type of brain was possessed by the common ancestor of the crossopterygians, dipnoans and amphibians, but the crossopterygians reverted to the ichthyic type.

" Neither of these alternatives is acceptable.

" With a view to emphasizing the character of the fore-brain, it is proposed to designate the whole of the fishes '*Archiprosencephalica*' and the rest of the Anamniota and the Amniota '*Neopresencephalica* [*sic*]'.

" *The history of the palato-pterygo-quadrate.*—The significance of the autostylic condition of the Amphibia and of the Dipnoi was discussed by Huxley, Bridge, Dollo, Goodrich, and Luther (1909, 1913, 1914), all of whom agreed that the autostylism was a secondary character. According to Edgeworth, Fürbringer was the first to cast doubts on the correctness of this view. He was 'of the opinion that the primitive condition was one in which the mandibular and hyoid bars articulated separately with the cranium' (Edgeworth).

" Edgeworth's opinion on the question is as follows: 'The sum of these skeletal phenomena suggests that Selachii, Batoidei and Teleostomi are descended from autostylic and monimostylic ancestors in which there was a pterygo-quadrate united to the chondrocranium at three points. The anterior end was probably fused with the ethmoid region. The middle region was probably fused with the trabecula by a basal process. The otic process was probably fused with the auditory capsule. This condition was lost and a streptostylic one was developed. *Heptanchus* is autostylic, the others amphistylic or hyostylic, whilst various traces are left in developmental phenomena or in adult anatomy of what existed in the past ' (*loc. cit.*, p. 257).

" In the main I find myself in agreement with Fürbringer and Edgeworth, though I cannot agree with the latter that any of the hyostylic elasmobranchs or teleosteans have descended from autostylic ancestors. I would point out that he has himself collected and produced evidence that, with the exception of *Lepidosteus*, *Petromyzon*, and two of the dipnoans, every anamniote, not excluding the Holocephali, sufficiently studied has an originally quite free palato-pterygo-quadrate cartilage (see Kesteven, 1931, Table I, p. 172). This should surely be interpreted to indicate that the primitive condition was a streptostylic condition. I cannot agree, however, that this primitive streptostylism was a hyostylism.

" Dollo wrote of the autostylism of the Dipnoi : ' c'est un pure conséquence de l'adaptation à un régime triturateur très accentué (mylodont), dans un but de consolidation de l'appareil masticatoir.

" ' 1. En premier lieu, la morphologie démontre, certainement, sans réplique, que les Vertébrés autostyliques dérivent de Vertébrés hyostyliques.

" ' Et l'Embryologie confirm cette conclusion.'

" This statement is supported by a quotation from Cope wherein Huxley is stated to have shown that the Batrachia are hyostylic in early stages and become autostylic in later stages of development.

" I have sought in vain for the embryological evidence that gives confirmation to the statement that autostylic vertebrata are derived from hyostylic forms.

" Kerr, too, is among those who believe that the primitive condition was one in which there was an attachment of the mandibular arch posteriorly.

" He states that ' the usually accepted idea of the mandibular arch is to regard it as a half-hoop shaped cartilage resembling the other arches, to which is added a forwardly projecting outgrowth—the palato-pterygoid bar—which forms the primitive upper jaw skeleton.'

" I have not met elsewhere this idea of an *added* palato-quadrate, nor can I find justification for the suggestion in the facts.

" There is, of course, growth in length of the maxillary segment of the first arch as there is growth in length of the mandibular, or as there is growth from the centre both ways in length of the branchial and hyoid arches, but this growth in length of the dorsal segment of the first arch is not fundamentally greater than in the other arches and does not suggest the addition of anything not added in the growth of the other arches.

" In its most primitive form, in the early embryos of elasmobranchs, the dorsal and anterior end of the first arch is almost in contact with the trabecula behind the rudiment of the nasal sac, lying close to the edge of the future mouth. With increase in size of the individual and the increasing gape, the upper and lower segments of the arch are lengthened proportionately, becoming segmented one from the other in the middle of the length of the arch just as do the other arches.

" As the upper segment grows forward it retains its close relation to the trabecula, and in some cases becomes temporarily continuous therewith, but it should be noted that this point of temporary continuity, or articulation, is not back close to the posterior end of the trabecula near the otic capsule, but anteriorly near the nasal capsule, either in front of, beneath, or behind it.

" The hinder end of the upper segment of this first arch does not become approximated to the skull base, but becomes attached to the lower end of the upper half of the second arch, hyomandibular.

" Turning now to the amphibians, it is clearly the forward end of the arch which so commonly becomes attached to and continuous with the lateral expansion from the forward end of the trabecula immediately behind the nasal capsule, whilst it is from the hinder end that are produced those processes, ascending, otic, and basal, whereby the posterior end of the bar becomes knit to, and continuous with, the trabecula, otic capsule, and parachordal cartilages.

" This hinder end is the morphological centre of the original arch, and is the point of fission into upper and lower segments ; it is not, as stated by Kerr, ' the dorsal portion of the original arch ' (*loc. cit.*, p. 320).

“ Now, of all the points of cartilaginous continuity, temporary or permanent, which have been noted between the rudiment of the mandibular arch and the neurocranium, this anterior one between it and the trabecula in the neighbourhood of the nasal capsule is the only one which has been found to occur in every one of the major divisions of the Anamniota, hence I have been led to believe that it is the most primitive.

“ In 1884 Cope described the structure of the skull of *Didymodus* and in the general discussion arising out of this study he expressed it as his opinion that the Holocephali were the most primitive of the elasmobranchs and traces thence the evolution of all the other fishes, the dipnoans and the amphibians. In the course of this discussion he quite plainly indicates that he regards the fixed upper jaw of the Holocephali as the primitive condition, for he says that these forms have not yet ‘ differentiated a suspensorium ’.

“ Portion of Kingsley's comment hereon is as follows : ‘ In this there are several important errors. In the first place the assumption that the monimostylic condition is the more primitive is at variance with every known fact relating to the comparative anatomy and embryology of the visceral arches.’

“ I believe that there is no room for doubt that the maxillo-mandibular apparatus has been evolved from a visceral arch essentially similar to the arches behind it, and similar to the branchial arches as we see them to-day. If this be so it is surely unreasonable to assume that the primitive jaw was one in which the mandibular segment was in structural continuity fore and aft with the neural cranium. There must have been transitional stages between the original arch and the attached arch ; there was surely the slightly modified, the more modified, and the completely metamorphosed arch.

“ If an originally ‘ floating ’ visceral arch has become structurally continuous with the cranium at two points, it is not unreasonable to assume that the nearest point of contact was the first to be converted to the continuous state ; undoubtedly the dorsal end was the nearest. Thus far I have the support of Kerr, but we differ as to what shall be interpreted as representing the original dorsal end of the arch in the amphibians.

“ Again, if the maxillo-mandibular apparatus has evolved from a visceral arch by the development and improvement of a joint at the point of division into dorsal and ventral halves, as a first or early step, then surely, as the first arch must have been attached to the second by muscular and fibrous tissue, the evolution of the protohyostylic condition should have been possible directly, without the intervention of a preliminary autostylic condition. Indeed had we but a few more examples of the incorporation of a portion of the hyoid arch into the basal attachment of the mandibular arch, as in *Neoceratodus*, we should have to assume that this was the primitive method of suspension. It is only the complete absence of any indication of the inclusion of any separate cartilages in the processes of attachment of the autostylic forms that justifies the assumption that this type of suspension has also been evolved directly from a primitive gnathostome as one of the original modes of fixation of the upper jaw posteriorly.

“ In the Teleostei we see the development of a metapterygoid process that may well be regarded as an incomplete attempt at autostylism, and, indeed, we have no evidence that it was not in this way, without any structural continuity between the maxillary and hyomandibular segments, that autostylism was developed.

“ In the present state of our knowledge, the final decision as to whether the greater probability is that the autostylic is an original or secondary mode of fixation of the maxillo-mandibular joint, must be by the personal equation. I am of the opinion that it has been evolved from a primitive suspension from the second arch, without that arch becoming modified to act as the suspensorium of the first.

“ However, whatever be the decision on this point, Edgeworth has left us little room for doubt that the autostylism of the Dipnoi and amphibians is a feature of fundamental importance in which these creatures differ from the fishes. This he has proven not only by his clear demonstration of the essential similarity and identity of the three processes of attachment, but also by his demonstration of the modification in the mode of development of the muscles of mastication in the amphibians and dipnoans on the one hand and the fishes on the other. His conclusion quoted above (p. 181) is fully justified by his evidence.

“ Though his main contention, as just stated, appears completely justified by his evidence, it is not so clear that he is correct in regarding the basal attachment as the most primitive, and the *processus ascendens* as being ‘ probably a later phylogenetic development ’.

"It must be pointed out that throughout the Amphibia, the *processus ascendens* is the first to develop, and that, with the exception of *Siphonops* and *Ichthyophis*, it presents identical relations throughout the class. On the other hand the basal process develops later, becomes attached later and presents varying relations to the neural cranium, as to its point of attachment, and to the nerves, and finally these variations show absolutely no relation, in their occurrence, to the natural grouping of the creatures themselves. (See Tables II, III and IV, Kesteven, 1931.)

"Our knowledge of the development of the processes of attachment in the Dipnoi is incomplete; unless the development in *Lepidosiren* is similar to that of *Ceratodus* it would seem that there are three different modes of development. Edgeworth states that in *Neoceratodus* the palato-pterygoid arises as an independent structure, and subsequently becomes attached by the same three processes as are found throughout the Amphibia. Agar has shown that in *Protopterus* the first chondrified portion is found as a spur from the trabecula behind the floor of the gasserian recess. His description and illustration of his findings in *Lepidosiren* indicate that it develops quite otherwise in this form, for, although he speaks of a basal attachment, it appears quite certain that in the earliest stage he illustrates the only attachment is by the *processus oticus*, and that a *processus ascendens* is present in the next stage.

"The condition in *Protopterus* is closely paralleled in *Petromyzon*, and, although I now think that one can place but little confidence in phylogenetic deductions based on the conditions in the cyclostomes, it is not entirely without significance that, as I have previously pointed out, the so-called basal attachment of *Petromyzon* is in truth by a *processus ascendens*, as judged by its position and relation to the nerves.

"Turning now to the evidence for an attachment by a *processus basalis* in the fishes, this evidence is very scanty, and fails to convince that it was of general occurrence in ancestral forms.

"In *Acanthias* Sewertzoff discovered that, prior to the establishment of the basal joint, there was continuity of the so-called basal process with the trabecula. This basal joint is, however, so far forward that it can hardly be homologized with the basal joint of the amphibians and the dipnoans.

"In *Lepidosteus* Veit found that the articulation of the maxillary rudiment with the basipterygoid process is preceded by a continuity in embryonic cartilage. In this case there appears no reason to cavil at the identification of the joint with that in the Amphibia.

"Unless the basal contact in *Gymnarchus* described by Assheton—and probably present in others of the Mormyridae (if one may judge from their adult structure as described by Ridewood) and in the Symbranchidae—can be regarded as homologous with the basal attachment of the amphibians, we have but one single instance of such a continuity among the fishes.

"The evidence for the homology of the spiracular cartilage and the otic process is more convincing. Personally, I incline to the opinion that the metapterygoid process of the Teleostei is also homologous with the spiracular cartilage, and therefore with the *processus oticus* of the dipnoans and the amphibians.

"It would seem that W. K. Parker and Bettany had the same inclination, for in the figures illustrating the chapters on the development of the Elasmobranch skull they consistently indicate the spiracular cartilage with the letters 'M.Pt.', and in the interpretation of the lettering these letters are translated 'metapterygoid' (Parker and Bettany).

"It therefore appears that either the attachment by the ascending process, or that by the *processus oticus*, is the most primitive of the three attachments of the amphibian autostylism posteriorly, but the evidence does not permit us to decide in favour of either.

"It would be of interest to learn whether the evidence of Edgeworth's wonderful series of *Neoceratodus* is such that his oto-quadrate cannot be regarded as a spiracular cartilage. Neither he, Allis, de Beer nor Schmalhausen appear to have considered the little pellicle of cartilage in this light.

"*The development of the vascular and respiratory systems.*—Since writing the earlier part of this section—the Dipnoi and the Amphibia—I have received a copy of Kellicott's paper. From that I learn that both he and Semon have expressed views relative to the evolution of the Dipnoi similar to my own, though they did not regard the Dipnoi as primitive amphibians.

"To my mind Kellicott's thorough and detailed work should have established the views of himself and Semon, and the scant attention bestowed upon his work by subsequent writers on the evolution of the Tetrapods, is a distinct reflection upon their ability to appreciate work in other branches of comparative anatomy and embryology than their own specialties.

" This review, of the features of anatomy and phenomena of development in the Anamniota which bear upon the evolution of the various groups, would be incomplete without a summary of the features of importance under the above heading, but for me to undertake such a review when Kellicott has presented the facts so well and briefly in his ' General Conclusions ' would be foolishness. I therefore quote that section from his work almost at length.

" ' It was stated in the Introduction that the immediate object of this investigation was to test embryologically the evidence, based upon anatomical considerations, for certain supposedly Elasmobranch and Amphibian characters seen in the adult vascular system of *Ceratodus*. Throughout the course of this paper, as the development of the vascular and respiratory systems has been reviewed, the embryological evidence has necessitated continual subtraction from the list of real Elasmobranch resemblances and continual addition to the list of Amphibian characters. For instance, the Elasmobranch similarities seen in the arrangement and distribution of the carotid arteries and the connection between the anterior carotid artery and the vessels of the hyoid arch, the double efferent branchial artery, the hyoidean gill, all prove to be in the nature of parallelisms and are preceded by Ganoid or Amphibian arrangements ; the arrangement of the veins of the head and of the lateral cutaneous veins resembles as closely the Amphibian as the Elasmobranch. On the other hand the Amphibian resemblances in the adult system all have been confirmed—the origin of the afferent branchial arteries, the arrangement of the epibranchial arteries, the relations of the lingual artery, the abdominal vein, the renal-portal vein, are typically Amphibian, and, excepting in the Cyclostomes, it is only in the Amphibian group (*Necturus*) that there is a continuity between the cardinal veins and the branches of the caudal vein, comparable with the arrangement in *Ceratodus*.

" ' Furthermore, embryologically the similarities to the Elasmobranchs were only in such characters as are common also to the Amphibia, for instance, the method of formation of the primitive aortic arch and the arrangement of the lateral cutaneous veins. But the Amphibian resemblances are extremely numerous—the method of mesoblast formation, the hypoblastic nature of the cardiac endothelium and the details of its formation, the development of the thyroid body, nearly all of the numerous details of the formation and development of the heart, the arrangement of the visceral arches, the nature of the gill-pouches and gills, the presence of elongate " larval gills ", the arrangement of the afferent branchial arteries and their relations to the conus, the early development of the branchial arteries, the formation and relations of the hyomandibular artery, the development of the lingual artery, the formation and relations of the carotid arteries throughout a long period, the relations between the posterior cardinal veins and the pronephros, the later condition of the posterior trunk veins, the development of the inferior jugular veins, the development of the abdominal vein, the arrangement of the vitello-intestinal vein and the formation from it of the hepatic and subintestinal veins, the formation of the hepatic-portal vein and its relations with the subintestinal vein, the development of the lung—in all of these respects, to enumerate only the more important, there is close, usually exact correspondence between *Ceratodus* and the Amphibia.

" ' Characters more or less intermediate between Elasmobranch and Amphibian arrangements are the number of gill pouches, the development of the efferent branchial arteries which resembles the Ganoid rather than the Amphibian, the arrangement of the interrenal veins, and the frequent anastomoses between the posterior cardinal veins . . .

" ' The immediate object of this investigation as stated above is, of course, really a part of the larger question of the relationships of the Dipnoi. It is unwise to attempt exact or complete statements in the entire absence of knowledge concerning the development of the Crossopterygii, especially since such knowledge is soon to be expected, but it is absolutely impossible to believe that the Amphibian resemblances seen in *Ceratodus* in the development of the vascular, respiratory and urinogenital systems, as well as throughout the early processes of development, are in the nature of parallelisms. In the light of their embryology, it is impossible to believe that the Dipnoi and the Amphibia are not closely related and that they have not travelled for a time along the same path at some period during their history.'

" When to this striking evidence are added the facts that these two groups are eupulmonate, autostylic, and neoprosencephalic, differing in all three respects fundamentally from the rest of the Anamniota, it may be fairly claimed that Kellicott's conclusion is as completely proven as circumstantial evidence *can* prove it.

"Finally, it is also contended that all the recent work on the development of the Crossopterygii and Dipnoi has indicated that the latter are more nearly akin to the Amphibia than to the former, and that this fact should be admitted in classifications by assigning the Dipnoi a place among the Amphibia.*

"The Evolution of the Cheiropterygium.

"The evolution of the cheiropterygium is so wrapped in obscurity that Kingsley's summary—'No known facts of either embryology or palaeontology throw any certain light on the matter'—is still very true. The latest survey of the question that I am acquainted with is that of Gregory, who briefly reviews the previous work.

"It must be admitted that Gregory is correct in his statement that: 'The endoskeleton of the pectoral limb of the Rhipidistian offers the only remote approach to the tetrapod type hitherto known among recent or fossil types'; and whilst one notes that he is in agreement with Patten, Broom, and Watson as to which elements shall be regarded as homologous with humerus, radius, and ulna, one also notes his choice of the word 'remote' and feels that therein he was wise.

"Gregory further expresses the opinion that the basal and central line of pieces in the fin of *Eusthenopteron* are probably homologous with the mesaxial series of *Neoceratodus*, and no reason is apparent why one should not agree with this suggestion.

"There is other evidence that the dipnoan fin was the starting point for the evolution of the tetrapod limbs, which, so far as I am aware, has not heretofore been advanced. I find that among the large number of fins which I have been able to dissect, the dipnoan fin alone is provided with a segmented musculature, the segments of which are placed along the length of the fin, on both sides thereof, so that the segments can be flexed independently.

"This extension of the muscle along the length of the fin was probably the first step in the development of the effectually jointed limb; certainly such an extension must have preceded the modification of the skeleton, and in all probability it caused the modifications. This excursion of the muscles along the axis of the fin was a more important factor in the evolution of the limb than the mere development of a fleshy muscular lobe at its place of origin from the body. The muscles of this basal lobe could but actuate the fin as a whole, and condition the more perfect development of the single joint. The fleshy lobe of the rhipidistian fishes was no greater than, if indeed it was as large as those of such typical forms as *Parascyllium collare* amongst the sharks and *Periophthalmus barbatus* amongst the Teleostei.

"The evidence is, indeed, so scanty that theorizing on the evolution of the tetrapod limbs amounts to little more than speculation, but the following summary is at least not unreasonable.

"The primitive limb was probably an archipterygium as defined by Gegenbauer, and it may have been derived from an external gill as postulated by Kerr. The concentration of muscle fibres at the base of the archipterygium caused the shortening and broadening of the structure with the ultimate development of the various types of ichthyopterygia. The development of muscular tissue along the length of the archipterygium and its segmental arrangement led to the improvement of the joints between the skeletal units, and to the development of the cheiropterygium.

"Though it may be that the homologies of the proximal pieces of the fin of *Eusthenopteron* are as suggested by Gregory and others, it is equally probable that the fin presents an early stage in the transition from the form with a single piece next the proximal element and those with three or more which are typical of the recent fishes."

---

* Three other features may now be added to this review.

The Squamosal bone of the Dipnoi, and in particular that of *Neoceratodus*, is so essentially similar, in all its relations to the chondrocranium and to the muscles of mastication, to that of such anuran forms as *Bufo* and *Calyptocephalus* that it is quite impossible to deny their complete homology.

Recently Dakin has shown that the osmotic index of the body fluids of *Neoceratodus* is that of an amphibian, and, moreover, that the striking difference between this index and that of the fishes is due to the concentration of urea in the fishes and its absence from the body fluids of the Dipnoans and of the Amphibians (Dakin, 1931).

Finally Dr. Bancroft has demonstrated that the young of *Neoceratodus* cannot be persuaded to live unless they be grown in an aquarium in which a shelving sandy "beach" is provided for them, so that they may rest with the mouth out of water just as the frog tadpole does.

2. The Evidence of their Cephalic Muscles on the Phylogeny of the Amphibia.

Since there are two conflicting views as to the origin of the Amphibia, it will be necessary to compare their musculature with that of the Teleosts and with that of the Dipnoi.

At the outset we cannot fail to observe that there is a very great difference in the ventral constrictors of the mandibular and hyoid segments of the amphibians and teleosts. True, in both there are Mm. submentalis and intermandibularis, but here the resemblance ceases. In the teleosts the posterior portion of the mandibular constrictor sheet has coalesced with the anterior portion of the hyoid sheet to form a protractor hyoidei, a muscle which is not developed in the amphibians.

It is a fact that in such a form as Pseudorriton the cerato-hyoideus externus and cerato-hyoideus anterior together simulate the protractor hyoidei of the teleosts, and that even the former muscle alone bears some resemblance to it, and it may be suggested with some justification that what we see is the protractor hyoidei derived from that anterior portion which, in the teleosts, is derived from the mandibular constrictor.

This resemblance is probably a parallelism superimposed on a partial homology. The essential fact to realize is that there is no evidence in the amphibian ontogeny of the suppression of a portion of the Csv.1. In the Selachians the Csv.1 develops as a continuous sheet. In the teleosts the sheet is divided to develop a submentalis, an intermandibularis and a portion of the protractor hyoidei (see p. 76-77).

In the Amphibians the sheet divides to develop a submentalis and an intermandibularis. Such a differentiation of the mandibular sheet into an anterior part, composed of fibres continuous from side to side—the submentalis—and a posterior part, composed of fibres which extend to the mid-line only—the intermandibularis—is already initiated in certain of the selachians and this division of the sheet is the only division found throughout the whole of the vertebrata, excepting only in the teleosts. It should be understood that the treatment of the mandibular sheet of the Selachians earlier in this work (p. 21), as consisting of a pars intermandibularis and a pars extra-mandibularis, is not based upon its development, but only on its adult relation to the mandible.

Therefore, to regard the cerato-hyoideus externus of the amphibians as being derived from the protractor hyoidei of the teleosts by the loss of the mandibular component, is to assume a return to a more primitive condition, whereas there is no reason to believe it could not have evolved directly.

This becomes the more apparent when we study and compare the ventral hyoid muscles in the two groups.

It will be remembered that the hyoid constrictor sheet in the teleosts is highly modified to form the complex hyohyoideus and that in this complex muscle it was not possible even to suggest what might be the boundaries between the superficial and deep constrictors which had contributed to its make-up.

In the Amphibians the superficial and deep constrictors are quite clearly differentiated, completely separate muscles, and it is probable that one is able to recognize the derivatives of the partes arcuata and interinscriptionalis of the elasmobranch sheet. Once more it is necessary to insist that the division of the Csv.2 of the elasmobranch into these parts was an anatomical convenience and not a developmental necessity, so that when we recognize the Csv.2 in an almost unaltered condition in the amphibians that is, perhaps, more than might have been expected, and surely indicates that its form in the Amphibia has been derived direct from the elasmobranch type without the intervention of a teleost stage.

The antero-posterior and laterad obliquity of the cerato-hyoideus externus which is responsible for the similarity of the muscle to the hyohyoideus of the teleosts, is really characteristic of the elasmobranch interhyoideus, and its attachment to the mandible close to the symphysis (per medium of the cerato-hyoideus anterior) is foreshadowed by the interhyoideus in the Holocephali. Here again there is no reason to suppose that the muscle as we find it in the amphibians could not have evolved direct from the Elasmobranchian condition.

Actually there is, then, no shadow of any teleostean influence to be found in the anatomy and/or development of these ventral constrictors.

Examination of the same muscles in the Dipnoi shows that they differ from those of the amphibians only in being more primitive. To argue that the muscles in the dipnoans are degenerate would also involve one in the assumption that their degeneration had taken the form of a return to the primitive elasmobranchian condition; the resemblance to that simple form is undeniable and inescapable and, moreover, there is here even less indication of any teleostean influence.

Having dissected, and otherwise studied, the several forms, I have to record that the arrangement of these muscles in the Dipnoi appeals to me as being very definitely the connecting link between the amphibians and the Holocephali.

The mandibular adductor muscles of *Neoceratodus* bear a striking resemblance to those of the Holocephali. It seems to be beyond question that these were, in both cases, derived directly from the elasmobranchian condition. There is little trace of that division and specialization of these muscles so characteristic of the teleosts.

It is not impossible that the little retractores anguli oris, which have been described in the two dipneumonous forms, are comparable with that portion of the temporalis which acts as a retractor anguli oris in the teleosts.

In the amphibians the depressor labii superioris of the anuran tadpole appears very certainly to be homologous with that portion of the temporalis which, in the teleosts, acts in like manner to depress the labial bones.

This, however, is not evidence of a teleost influence, but rather that the utilization of the labial cartilages as a framework in connection with oral prehension had already taken place in the common ancestor of both groups. Clearly they are so used in the Holocephali.

Apart from this similarity, there is no trace of any evidence that the muscles of mastication of the amphibians have evolved from a teleostoman type. Their specialization is sui generis and not moulded on the teleostoman.

The depressor mandibulae is very definitely foreshadowed in the Holocephali, where its origin from the dorsal part of the hyoid superficial constrictor is beyond question. Here again we find no trace of any teleostean influence in the evolution of the muscle. There is nothing comparable to the depressor mandibulae in any teleost that has as yet been described.

Amongst the intrinsic branchial muscles we certainly find that the ventral branchial muscles—subarcualia obliqui, transversi and recti—are essentially similar to these muscles in the teleosts and have no parallel amongst the muscles of the branchial segments in the elasmobranchs. On the other hand, the musculi marginales of the Dipnoi and Amphibia are derived from the interbranchial muscles of the elasmobranchs, and these muscles are not developed in any teleost. It is difficult to understand how these muscles could have reappeared in the amphibians if they are descended from teleost ancestors, for the muscles are very completely discharged from the whole of the developmental history of the teleosts. It will be remembered that in these forms the branchial muscle plates split into dorsal and ventral portions and that there remains no connecting strand between the two halves. To assume that in the descendants of such forms this splitting should have been abandoned and the older method of developing a muscle from the middle segment returned to, is an assumption that evolutionary roads may be travelled backwards as well as forward, an assumption entirely contrary to the great mass of the evidence available; so much so that it is almost repugnant to the modern morphologist. Moreover, the assumption would be invoked on behalf of relatively unimportant evanescent muscles.

The amphibians also differ from the teleosts in the complete absence of the epiarcual muscles; herein, of course, they also differ from the elasmobranchs.

The conflicting evidence of the branchial muscles is probably to be explained by the fact that both the teleosts and amphibians are descendants of a form in which the dorsal branchial muscles, the interbranchial muscles, and the ventral branchial muscles were all developed. The teleosts lost both the dorsal and interbranchial, the amphibians lost only the dorsal.

If my identification of the superficial dorsal constrictors of the amphibians is correct, then this is a further point in which they differ from the teleosts; if, however, these should prove to be in reality the levatores arcuum branchialium, as has been said in the past, then the resemblance here is to both the teleosts and the elasmobranchs.

Generally the conclusion that seems forced upon us by a comparative study of the cephalic muscles of the teleosts, dipnoans and amphibians is that there is no evidence either in their development or adult anatomy to indicate a teleostean ancestor for the Amphibia.

On the evidence before us, we are therefore justified in stating that the Dipnoi were probably derived directly from some elasmobranchian, or pre-elasmobranchian ancestor without any direct inheritance of teleostome characters, except such as were present in a more ancient common ancestor. And we may further state that the evidence points to the Dipnoi as presenting the most primitive definitely Amphibian form known, and that it probably approximates to the direct ancestor of the known Amphibia.

These conclusions, however, do not complete a review of the probable origin of the Amphibia, for the Embolomerous skull is so different from that of the rest of the class that one is practically forced to the conclusion that there are, amongst the fossil and recent forms, representatives of three very distinct tribes—the Embolomeri, the Dipnoi, and the remainder of the class.

Unfortunately, we are denied any knowledge of the Embolomeri except of their skeleton. The skull, however, presents differences which are here believed to be fundamental, and these we proceed to discuss.

3. The Serial Homology of Certain Bones in the Skulls of Amphibia and their Bearing on the Evolution of the Class.

The Amphibian skull presents itself in two very distinct forms. On the one hand, there are the skulls with expanded pterygoid bones related to the basis cranii, and, in all probability, developed in that relation in all the forms in which they are found, certainly as developed in the Dipnoi. Skulls of this type are found in the Embolomeri and the Dipnoi.

On the other hand, there are the skulls with a pterygoid bone completely, or almost completely, divorced from the basis cranii, and in all the recent forms, if not also in all the fossil forms, developed in relation to the pterygoid process of the quadrate, and only gaining such relation to the basis cranii as it possesses by later, secondary, growth.

It is significant that the Embolomeri, which present the former type of palate in its highest development, are remarkably similar to the Cotylosaurian Reptiles, and have been regarded by all who have studied them as probably presenting the amphibian type from which the Reptilia generally have evolved.

It is submitted that the two very distinct types of amphibian skulls are at once understandable if they be regarded as being derived by two different lines of evolution from a condition such as is presented by the Dipnoi.

On the one hand, there evolved the primitive " fish " type of palate with (1) a broad parasphenoid, (2) poor ossification of the basisphenoid region of the basis cranii, (3) a so-called pterygoid which presents three rami, bounds the via masticatoria medially and anteriorly, is developed in relation to the pterygoid process of the quadrate and gains such relation to the basis cranii as it presents by later, secondary, growth.

On the other hand, there evolved the more advanced " tetrapod " type of palate with (1) the parasphenoid reduced to a " vomerine " splint, (2) good ossification of the basisphenoid region of the basis cranii, (3) the pterygoid bone, expanded and contributing largely to the formation of the palate, occupying much of the situation of the broad parasphenoid of the more primitive type of palate, meeting its fellow in a more or less lengthy median suture, suturing with the median edges of the palatine and os transversum, bounding the via masticatoria medially and developed, in all probability, in relation to the basis cranii.

These two types of amphibian palate are represented by the Embolomeri on the one hand and the rest of the Amphibia on the other, with the Dipnoi as a connecting link between them.

It must be quite obvious that certain statements as to the situation, relations, and development of the " pterygoid " bone in the two types of palate suggest that they are not homologous.

At the outset one may say with confidence that the bone which has been designated pterygoid in the whole of the Amphibians, excepting the Dipnoi and the Embolomeri, is the same, and that the bone is homologous throughout. Its development has been observed in a sufficiently representative range of genera to permit one to assert this with confidence.

Comparison of the bones in a representative range of fossil palates serves to confirm the homology throughout the fossil forms.

On the other hand, one is also unable to deny the complete homology, one with the other, of the pterygoid bones of the Embolomeri and the Dipnoi.

When, however, the pterygoid bones of these last are compared with those of the other amphibian palates it becomes almost obvious that the bone in the two groups is not the same. The development of that of the Dipnoi has already been discussed (p. 201) and it appears entirely reasonable to assume that the pterygoid of the Embolomeri is developed in similar manner in relation to the ethmoid and sphenoid regions of the basis cranii. It is probable that the meeting of the pterygoids ventral to the "vomerine" parasphenoid is the result of secondary growth, and that like those of the Dipnoi they appeared first on each side of the much reduced parasphenoid.

To the present writer it seems probable that these median pterygoids of the "tetrapod" type have arisen by the division of the primitive parasphenoid into three parts. The Dipnoi are believed to represent a primitive condition in this division. The subotic wings of the bone are believed to have developed from their own centres of ossification, whilst the median portion has been developed from a third centre. It is for this reason that the parasphenoid has been so constantly designated the synpterygoid throughout this work.

It is further believed that the so-called pterygoids of the great majority of the amphibian palates are not homologous with these but are homologous with the os transversum of the reptilia. But, it will be at once asked, are not those bones already present in the palates of certain of the Stegocephalians, and if so how can it be that these forms possess two ossa transversa ?

An examination of the stegocephalian palates in question, and a comparison of them with other closely related palates discovers that this os transversum is only present in quite a few of the stegocephalians. The bone is said to be present in *Eryops*, *Capitosaurus* and *Metoposaurus*, may be present in *Rhinesuchus* and *Trematosaurus*, and is certainly absent in *Batrachosuchus*, *Cyclotosaurus* and *Branchiosaurus*. It is apparently also absent from the palate of *Archegosaurus*. The os transversum is apparently present in *Orthosaurus*, but its shape has been differently determined in each of the three descriptions available to me. Watson says that in the closely allied *Pteroplax* there is no os transversum, "the palatine extending back to the end of the maxilla".

Clearly, if there be a bone in the lateral portion of the palate behind the palatine in any of the stegocephalian palates, it cannot be regarded as an established component of the palate, but as an adventitious element. Watson has suggested that there is evidence that in *Orthosaurus* this variability is carried still further by the division of the bone into two.

In order that a proper understanding of the os transversum be arrived at, it becomes necessary at this stage to anticipate later work and examine the bone in the reptilian palate.

At the outset it is found that the bone is certainly absent from most of these most primitive reptiles, the Cotylosauria. It is "possibly" present in *Seymouria* and *Pariasaurus* alone amongst the members of this group.

The bone is also absent from the palate of the Testudinata and from that of the Ichthyosauria.

It is present in all other reptilian palates.

Though at first sight the transpalatine bone of such a reptile as *Thaumatosaurus* or *Amphistraena* bears a close resemblance to the bone so named in some of the Stegocephalians, a closer examination reveals that here, as in the great majority of the reptiles, the os transversum sutures with the lateral edge of the pterygoid well behind its anterior end, whereas in all the stegocephalians the os transversum lies in contact with the anterior end of the pterygoid and, further, it will be observed that the pterygoid lies to the inner side of the subocular palatal vacuity where it sutures with the os transversum in the reptilian palate, but to its outer side in the Stegocephalians.

It is, of course, quite impossible to prove this contention, but it is believed that the explanation of the seeming discontinuity and apparent variability lies in the fact that the os transversum of the reptilian palate is really the homologue of the anterior portion of the pterygoid bone of the generality of the Amphibia.

The so-called os transversum of the Stegocephalians might be designated post-palatine, if this belief be correct.

The evidence on which this belief rests may be briefly reviewed :

(1) The primitive condition of the covering of the basis cranii was by an expanded parasphenoid, which covered the whole of the basis of the cavum cranii and extended forward below the sphenoid and ethmoid regions.

(2) The development of endochondral ossification in the basisphenoid region was accompanied by a reduction of the parasphenoid bone ; probably this was a causal correlation.

(3) The reduction of the parasphenoid is associated with the development of pterygoid bones which, in all the most primitive reptiles, the Embolomeri and the Dipnoi, occupy the situation of the lateral portions of the primitive parasphenoid posteriorly and the whole of the anterior portion, excepting only the narrow vomerine splint-like remnant.

(4) The primitive form of the pterygoid bone is an expanded lamina which meets its fellow in the mid-line.

(5) Throughout the Amphibia, excluding only Embolomeri and Dipnoi, the so-called pterygoid articulates with the subotic region of the basis cranii, in the neighbourhood of the basal root of the quadrate.

(6) Throughout the Reptilia and in the Embolomeri the pterygoid articulates with the basisphenoid and commonly also with the subotic portion of the base of the cranium. The articulation with the basisphenoid is the only relation to the basis cranii which is constant.

(7) Throughout the whole of the Amphibia, excepting only the Embolomeri, the so-called pterygoids are widely separated anteriorly and lie laterally to the subocular palatal vacuity.

(8) Throughout the whole of the Reptilia and in the Embolomeri the pterygoid bones meet at, or are very closely approximated to, the mid-line anteriorly and lie medially to the subocular palatal vacuity or are so extensive as to close that vacuity.

(9) The primitive pterygoid bone exhibited by the Dipnoi is developed, like the parasphenoid bone, as a membrane bone on the ventral surface of the cavum cranii.

When to these facts there is added the sum of those many features which indicate that the Dipnoi are primitive, the most primitive Amphibians known, and that they probably approximate very closely to the common ancestor of the whole of the Amphibia, it appears reasonable to conclude that the final total justifies the belief that the pterygoid bones of the Reptilia are derived from the primitive parasphenoid and are not homologous with the pterygoid bones of the Amphibia, excepting only those of the Dipnoi and the Embolomeri.

The recognition of the os transversum of the reptilian palate as the homologue of the pterygoid of the amphibian rests largely on the acceptance of the last belief.

If the reptilian pterygoid really represents, and is to that extent homologous with, the lateral part of the parasphenoid of the amphibian palate, then the os transversum is at once recognizable as the anterior arm of the typical amphibian pterygoid. Throughout the whole of the Amphibia, excepting only the Embolomeri and the Dipnoi, this pterygoid bone acts as the bony boundary of the via masticatoria on its inner and anterior margins, and serves also as a strut maintaining in place the maxillary arcade at the anterior limit of that space. It will be at once granted that such a limitation of the " via " and such a strut to the arcade are mechanical necessities, and that, once developed, the structure would be maintained. The anterior boundary of the via masticatoria is the posterior boundary of the orbit. In the absence of a rigid bar between the two, contraction of the anterior muscles of mastication would result in their displacing the structures in the orbit forward or compressing them against the anterior boundary of the orbit.

In the apode Amphibia we observe the so-called pterygoid bone reduced to the reptilian (os transversum) condition, a short bar extending from the posterior end of the palatine mediad and caudad to articulate with the lateral edge of the parasphenoid and closing the via masticatoria anteriorly. In this form the articulation with the basis cranii in the region of the basal root of the quadrate has been lost by reason of the fact that the parasphenoid has extended laterally beyond the limit of the basis of the cavum, and the relation to the basal root of the quadrate has also been lost. On the other hand, the bone is closely related to a persistent, ossified, pterygoid process of the quadrate, which lies above its posterior end articulating with the same narrow subocular flange of the parasphenoid.

It is unquestionable that, were the parasphenoid of the Apoda divided into right and left halves we would quite unanimously agree that the so-called pterygoid should be regarded as an os transversum ; all its relations to bony and soft structures would be as in the reptiles.

It would appear that the strong development of the muscles of mastication had necessitated greater space, and that this had been obtained by the forward transportation of the anterior boundary of the via masticatoria, whilst the development of a lateral subocular flange of the parasphenoid had divorced the inner end of that bar from the basis cranii.

In similar manner, it is believed, the splitting of the parasphenoid bone into right and left halves and their separation from the basis cranii has determined the lateral migration of the os transversum in the reptilia, whilst the development of massive muscles of mastication has forced the bone forward.

It is submitted on behalf of the arguments just advanced, that they do not run contra to any evidence of palaeontology, embryology, osteology, or myology, and that they provide an explanation quite in harmony with both phylogeny and teleology.

Since, however, it is not contended that the homologies here suggested are proven beyond question by the facts adduced in evidence, it is desirable to examine briefly those facts which would appear to contradict the conclusions arrived at.

Probably the, apparently, most contradictory fact is that in some reptiles the pterygoid bone develops in relation to the pterygoid process of the quadrate in a manner similar to the development of the pterygoid of the Amphibia.

A critical examination of the conditions of this relation throughout the Sauropsida reveals that the resemblance is probably more apparent than real. As a matter of fact, the association of the pterygoid process and the pterygoid bone is not of general occurrence in the group ; it is actually the exception and not the rule. There is no such association in any of the Aves at all, and there is no doubt as to the complete homology of the bone in the two subclasses.

In the Crocodilia the pterygoid bones are developed in relation to the lateral edge of the basis cranii, exactly as postulated for the lateral portion of the parasphenoid, nor does it present any relation to any part of the quadrate.

In the Chelonia the relation to the pterygoid process of the quadrate is one of juxtaposition only, there is no actual ectochondral ossification.

In the Lacertilia, though there is, in some genera, a close association of the posterior end of the pterygoid bone and the pterygoid process in the neighbourhood of the epipterygoid cartilage, the complete absence of any such association in other genera, by reason of the complete absence of the pterygoid process itself, may be taken as evidence that there is no ectochondral ossification of the process even in those cases in which the process is present and closely placed to the pterygoid bone.

In the Ophidia the pterygoid bone is developed quite independently of any cartilage at all.

In *Sphenodon*, the only recent Rhynchocephalian, Howe and Swinnerton have very clearly demonstrated the first appearance of the pterygoid bone as an ectochondral ossification of the median and lower surface of the pterygoid process.

There is room for doubt that the pterygoid process of the Reptilia is the same thing as the process in the Amphibia, but assuming for the purposes of the present discussion that there is no doubt about the homology of the processes in the two classes, it must be admitted that the variation observable in the relation of the bone to the process within the Sauropsida at least suggests that the relation is not genetic, but is spatial only.

It may be pointed out that, if the pterygoid bone is, as here suggested, derived from the lateral portion of the parasphenoid and has been moved laterally, it must have become approximated to the quadrate, and may well have acquired secondary relation to the portion of the quadrate it came in contact with.

A critical examination of the facts of the development of the pterygoid bones in the Sauropsida reveals that in the great majority of the members of the class there is no genetic relation between the pterygoid bone and the pterygoid process.

If the facts be viewed with the idea that the pterygoid bone of the Sauropsida is homologous with that of the Amphibia, then, since the pterygoid bone is always developed as an ectochondral ossification of the process throughout the Amphibia, the occasional occurrence of this relation amongst the Sauropsida will be regarded as significant, and as the primary relation. If, on the other hand, one is able to view the facts without this bias, it has to be admitted that the weight of evidence of the known ontogeny of the bone amongst the Sauropsida indicates that the occasional occurrence is a secondary relation.

Actually the relation only appears in *Sphenodon* and in some Lacertilians.

It may be pointed out, as contradicting the homology here suggested, that, whereas the amphibian pterygoid bone is always developed in genetic relation to the pterygoid process, the reptilian os transversum never is.

Whilst this is quite true, it seems that it may be quite simply explained by consideration of the changes which have taken place in its situation, and of the forces which may be assumed to have been responsible for those changes. In its transposition from its posterior to its anterior situation, the bone has been divorced from the much reduced pterygoid process. The need for the rigid support and limitation to the muscles of mastication is assumed to have conditioned the retention of the anterior arm of the pterygoid as the muscle mass increased in size, to meet the demands of more active modes of living and greater strength for mastication. The cartilaginous process was reduced, as we know from the evidence available, but the bone was retained.

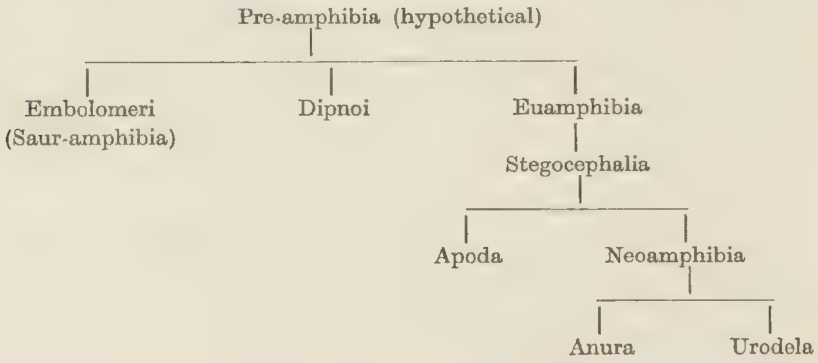
Finally, it may be remarked that it is not without significance that in the only Amphibians in which the basal and otic processes of the quadrate are not developed, the so-called pterygoid bone has lost its relation to the basis cranii in the region where the basal process would have been attached, and has been transported forward. The reference here is, of course, to the Apoda. Is this not an indication that the loss of these attachments of the quadrate is causally related to the changed position of the os transversum ? The processes in question are never present as part of the quadrate in any of the Sauropsida. Did the liberation of the quadrate condition the liberation of the os transversum also ?

Finally, it may be argued that the rachitomous palate as exemplified by *Eryops* presents a connecting link between the typical amphibian and the cotylosaurian condition as exemplified by *Seymouria.* At first sight it would appear that the only modification of the latter skull needed to bring about the condition in the former is that the admedian portions of the pterygoids should disappear between the lines joining the spicule of the bones between the palatine and prevomer and the basitrabecular process. This, however, is not so ; such a view would entirely overlook the fact that the parasphenoid in the cotylosaurian skull has been reduced to a vomerine splint, a fundamental difference between the two skulls, and it would also overlook the fact that, whereas the pterygoid of *Eryops* articulates with the parasphenoid and subotic portion of the skull, in the cotylosaurian, the articulation is with the basitrabecular process* lying anterior to the otic capsule.

As a matter of fact, *Eryops* presents a typical rachitomous palate ; its apparent resemblance to that of the Cotylosaurians is due only to the extension of the pterygoid bones anteriorly. Were it to lose that little piece of the bones which extends anteriorly to the palato-prevomerine suture it would lose entirely its apparent resemblance to the Cotylosauria.

There is, then, evidence of two distinct lines of descent presented by the Embolomeri on the one hand and the remainder of the Amphibia on the other.

The evidence of their cranial osteology, musculature and development suggests the following broad classification of the Amphibia.



---

* It is a fact that a basitrabecular process has been stated to be present in the skull of *Eryops*, but the statement is based on a confused idea of the true nature of the process. It is obvious that the process so designated lies too far back to be a true basitrabecular process, and, moreover, the process is parasphenoidal with a lateral expansion of the basisphenoid above it.

PART III. THE SAURIA.

THE REPTILIA.

INDEX OF THE ABBREVIATIONS USED ON THE ILLUSTRATIONS TO PART III.

A., Arytenoid cartilage; A-i., M. aryteno-interthyroideus; C.c.s., M. constrictor colli spinalis profundus; Chy., Ceratohyoid cartilage; C.la., M. constrictor laryngis; Clm., M. cleidomastoid; Csd.2a & 2b, The dorsal hyoid superficial constrictor muscle; Scv.1a & 1b, M. intermandibularis; Csv.1b′, M. interhyoideus; Csv.2a & 2b, The ventral hyoid superficial constrictor muscle; Csv.2′, The ventral hyoid superficial constrictor muscle; Csv.2″, Constrictor colli spinalis; C.thy., M. ceratothyroideus; D., the dentary bone; Di.la., M. dilator laryngis; D.m., M. depressor mandibulae; D.m-m., M. depressor mandibulae mandibularis; G.g., Gasserian ganglion; G.gl., M. genioglossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.gl.a., M. interhyoideus; H.gl.p. & Hg.p., M. hyoglossus posterior; Hy., The body of the hyoid; Hy.m.l. & Hy.mn., M. hyomandibularis lateralis and medialis; I.ch. & I.chy., M. interceratothyroideus; I.hy., M. interhyoideus; Ins.mass., The area of insertion of the M. massetericus; I.t., Interthyroid cartilage; Ju., The jugal bone; L.d., M. latissimus dorsi; Lg.d., M. longissimus dorsi; Lv.Oc., M. levator bulbi oculi; Lv.q., M. levator quadrati; M. & Mm., M. massetericus; M.e., M. interhyoideus; M.chy., M. ceratothyroideus; M.hy.h., M. hypohyalis; M.hy.m., M. hyomandibularis; M.q-m., M. quadratomandibularis; M.sp.pt., M. sphenopterygoideus; M.t., M. temporalis; Mx., The maxilla; Nv.d.p., The nerve to the M. depressor palpebrae; Nv.pt.int., The nerve to the M. pterygoideus internus; Nv.′, The ophthalmicus profundus branch of the fifth nerve; Nv″., The maxillary branch of the fifth nerve; Om., M. omohyoideus; P. & Pal., The palatine bone; P.c., P.n. & P.n.o., Partes cephalognathica and notognathica of the M. depressor mandibulae; Pila.ant., The pila antotica; P.l.a., M. protractor laryngis anterior; P.l.p., M. protractor laryngis posterior; Po., The postorbital bone; Pr.la., M. protractor laryngis; Pt.ex., M. pterygoideus externus; Pt.int., M. pterygoideus internus; Pt.,m. M. pterygoideus medius; Pt.i.l. & Pt.i.m., Lateral and medial parts of the M. pterygoideus internus; Pt.p., M. pterygoideus posterior; Q.a.a., The anterior arm of the quadrate bone; Q.h., The articular head of the quadrate; Q.j., The quadratojugal bone; Q.m., M. quadratomandibularis; Q.p.a., The posterior arm of the quadrate; Qu., The quadrate bone; R.a.o., M. retractor anguli oris; Re.la., M. retractor laryngis; Sc., The scapula; S-m., M. sternomastoideus; S.m., The symphysis menti; Sp.pt., M. sphenopterygoideus; Sq., The squamosal bone; S.t., The sheath of the tongue; St., The sternum; St.hy., M. sterno-thyroideus; St.hy.m. & St.m., M. sterno-thyroideus medius; St.l., M. sterno-thyroideus lateralis; St.p., M. sternothyroideus posterior; T. & Temp., M. temporalis; T.a., M. thyro-arytenoideus; Th., the thyroid cartilage; Th.gl., M. thyro-glossus; Th.mn., M. thyro-mandibularis; Th.ph., M. thyro-pharyngeus; T.hy. & Th.hy., M. thyro-hyoideus; Thy. & Th.c., the thyroid cartilage; Th.v., M. geniohyoideus; T.i., M. thyro-interhyoideus; T.m., M. thyromandibularis; T-m., M. temporo-massetericus; Tr., M. trapezius; Ty. & Ty.m., The tympanum; Ur., The urostyle.

ELASMOBRANCHIATA.	SAUROPSIDA
Csv.1a	M. submentalis.
Csv.1b	M. intermandibularis.
Dsv.1b^{2} (p. extramandibularis)	Not a separate entity
Pterygoideus	Mm. pterygoideus externus, medius and internus, and depressor mandibulae mandibularis
Quadratomandibularis ..	Mm. retractor anguli oris and temporo-massetericus, i.e. Mm. temporalis, massetericus and quadrato-mandibularis
Levator maxillae superioris ..	Mm. pterygo-quadratus, sphenopterygoideus and levator-quadrati
Csd.2a	M. depressor mandibular pars notognathica
Csd.2b	Mm. depressor mandibulae pars notognathica. Constrictor colli facialis (dorsal part)
Cpr.d2 (pars quadrato-hyoidea)	M. depressor mandibulae, pars cephalognathica
Levator hyoidei	? Cerato-hyoideus capitis of *Chelodina*
Interhyoideus	Interhyoideus
Csv.2a and 2b	M. constrictor facialis ventral part

1. **Lacertilia.**

Physignathus.

(Figs. 130–134.)

This is a large Agamid lizard; the species here described, *P. lesueurii*, is very common along the streams in the neighbourhood of Bullahdelah, N.S.W. The eggs are deposited in early November along the elevated banks of the stream. As many as twelve have been found in the one hole. It would appear that all are deposited before the hole is filled in, for a lizard caught in the act of oviposition had laid eight and they were not covered at all. The hole is about six inches deep, and the top eggs are only one to two inches below the surface. The eggs hatch out during the following February. I have been fortunate in obtaining nearly two hundred of these eggs in various stages of development. Two full sets of twelve were obtained immediately after being laid, and these were hatched for definite periods and then fixed. Two eggs collected as soon as laid hatched out in 109 and 105 days.

My developmental stages are numbered 1 to 100, the numbers indicating actually or very closely the number of days hatched. The series is complete from day to day, for the period three days to twenty-six, thereafter the hatching period was determined by comparing the state of development of single specimens from groups already partly hatched, with this early series and letting the remainder hatch on; as sets comparable with those already dated came to hand I was able to extend my series with close approximation to accuracy.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

(Figs. 130–131.)

The Depressor palpebrae inferioris.

This is a very thin sheet of radiating fibres which arise from a restricted area of the fibrous wall of the orbit, behind and laterally to the investment of the optic nerve as it enters the orbit, and spreads out in the lower eyelid superficially to the tarsus.

Innervation.—This is by a fine branch of the ramus mandibularis V which is given off from the gasserian ganglion before the R. mandibularis and R. maxillaris separate, but it may be traced through the ganglion to the mandibular ramus. It passes directly forward to the orbit, deep to the lower part of the pterygoideus externus muscle.

The Mandibular ventral constrictor (Csv.) is in two separate sheets, a smaller deep, the Submentalis, and a more extensive superficial, the M. intermandibularis.

The Intermandibularis (Fig. 130, Csv.1b) arises from the inner surface of the mandible anteriorly and from the outer surface posteriorly. The origin from the inner surface commences one-quarter of the full length of the mandible behind the symphysis, and terminates a little way behind the mid-point of the length of the mandible. This line of origin is fairly high up along the inner surface and is interrupted by four slips of the thyromandibularis which, coming from a deeper position posteriorly, perforate the intermandibularis to gain insertions on to the inner edge of the narrow inferior surface of the mandible.

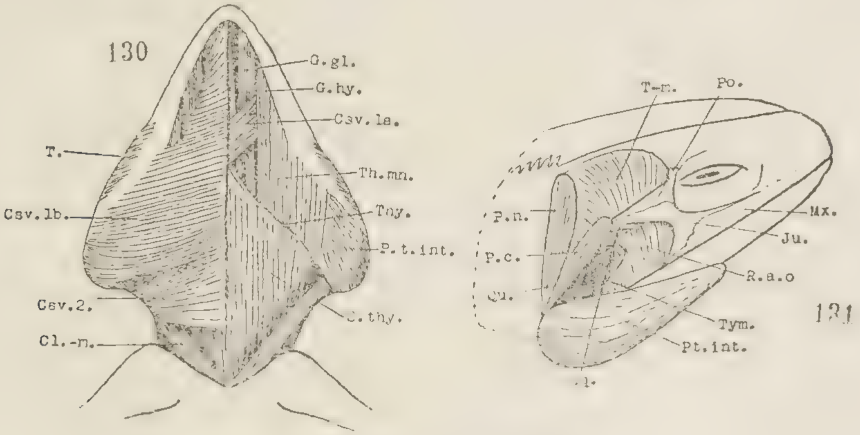
The origin of the muscle from the outer surface of the mandible commences where the other origin terminates and extends back to the tip of the post-articular process. In its anterior portion this origin is from the mandible between the M. pterygoideus internus and the insertion of the M. temporo-massetericus. Behind this the origin has been carried dorsally, by the swelling of the body of the former muscle and its insertion, to the inferior margin of the tympanic ring; behind this again the origin returns to the mandible between the depressor mandibulae above and the pterygoideus internus below.

Innervation.—This is by two separate branches of the R. mandibularis. After giving off the various branches to the masticatory muscles, the nerve enters the mandible on its inner side behind the coronoid process through Meckel's fossa, a small sensory branch being given off from its outer side just before it enters the canal. Inside the canal, after a short course, a branch is given off which passes down internal to Meckel's cartilage and then turns mediad and perforates the bone. This is, apparently, entirely motor, and it spreads its twigs out over the ventral surface of the muscle; it issues from the mandible ventrally to the last section of the origin of the muscle from the internal surface of the jaw. This, which Lightoller designates the mylo-hyoid nerve, supplies the motor twigs to the greater part of the intermandibularis.

After giving off this motor twig the main nerve continues forward in the canal till it reaches almost to the anterior limit of the origin of the intermandibularis pars superficialis. Here two more twigs are given off in quick succession. The first is the larger ; like the mylo-hyoid nerve, these also emerge from the bone ventrally to the origin of the muscle. The first of these two twigs is the lingual nerve, it perforates both superficial and deep intermandibular muscles and joins the hypoglossal nerve in the sublingual ganglion. The second may be termed the anterior mylo-hyoid nerve ; it divides into two branches, the first of which spreads out on the surface of the superficial intermandibular muscle to supply the anterior portion. The other branch perforates the superficial muscle and spreads out on the ventral surface of the deep part of the muscle (M. submentalis) supplying its motor nerves.

The Submentalis (Csv.1a) is a much smaller sheet of fibres which arise from the inner surface of the jaw dorsally to the origin of that portion of the superficial muscle which arises in front of the first perforation by the thyro-mandibularis.

Innervation.—This has been given in connection with that of the intermandibularis muscle.



Figs. 130-131.—*Physignathus.*

Insertion.—Both muscles are inserted into the mid-ventral raphe. The anterior fibres of the intermandibularis run sharply forward and are inserted almost at the symphysis, those immediately behind gradually, but rapidly, assume a directly transverse direction, and this is maintained to the posterior margin of the muscle. The fibres of the submentalis pass obliquely caudad, towards the mid-line and they are inserted into the same raphe deep to that part of the superficial muscle which arises in relation to the first, second and third perforations by the thyromandibularis. There is no indication of an interruption in the continuity of the superficial sheet immediately on either side of the mid-line.

The Retractor Anguli Oris is a muscle which, so far as I am able to learn, has not previously been recorded in any reptile. It is probably homologous with the massetericus minor of the Anura.

The muscle is a flat, roughly quadrangular, sheet which arises from the inferior edge of the squamosal bone and the inferior edge and deep surface of the jugal bone. The fibres pass directly ventrad to be inserted into the tissues of the lips at the angle of the mouth. There is no merging of this muscle with the underlying M. temporo-massetericus or pterygoideus externus muscles.

Innervation.—This is by a branch of the R. mandibularis V which reaches the muscle by passing rostrad and ventrad, deep to the temporo-massetericus, and then, turning laterad and rostrad between that muscle and the pterygoideus externus, it turns caudad around the anterior surface of the temporo-massetericus, to reach the deep surface of the retractor anguli oris.

The Temporo-massetericus is a very massive muscle which arises from the anterior surface of the quadrate, the anterior and dorsal surfaces of the parotic process, the anterior membranous wall of the auditory meatus, the lateral wall of the skull, both inner and outer surfaces of the posterior arm of the parietal and of the little post-temporal plastered to its ventral edge laterally, and finally from the upper part of the inner surface of the jugal and inner surface of the posterior arm of the post-orbital. The mass of the muscle fills almost the whole of the superficial area of the supra-temporal space, only a quite small area of the pterygoideus externus being visible in the antero-medial corner of the space. The whole of the fibres converge to be inserted on to the superior edge and outer and inner surfaces of the mandible from the tip of the coronoid process almost back to the joint. The insertion on to the outer and inner surfaces extends about half-way down the depth of the mandible ; the insertion on to the coronoid tip is in part effected by the tendon of the pterygoideus internus as was seen in some urodeles.

Innervation.—This is by several short branches which leave the R. mandibularis V just after that nerve separates from the ganglion.

The rest of the masticatory muscles form an exceedingly complicated and powerful pterygoid muscle which is not divided into parts by any definite cleavage planes. It is, however, necessary to describe it in three portions, anterior, medius and posterior. The Anterior, Pterygoideus externus, arises from the side of the body of the parietal and from the posterior surface of the post-orbital arm of that bone and from the greater part of the length of the epipterygoid bone. These fibres are gathered to a central tendon by which they gain an insertion on to the coronoid process of the mandible and the inner surface below it. This latter insertion is behind the coronoid process and also just behind the ventral process of the pterygoid and transverse bones.

This portion of the muscle corresponds very closely, and is doubtless homologous with the anterior portion of the pterygoid muscle of the amphibians.

The median portion, Pterygoideus medius, arises from the outer surface of the posterior process of the pterygoid bone and from the lower half of the anterior membranous wall of the auditory meatus as well as from the lower part of the anterior surface of the quadrate. These fibres are all inserted directly into the inner surface of the mandible over its full depth behind the coronoid and below the insertion of the temporo-masseteric fibres inserted on the inner side of the mandible. There is no clear plane of separation between these and the more superficial temporo-masseteric fibres.

The posterior portion is the homologue of the muscle which, in *Sphenodon*, Edgeworth designates the pterygo-mandibularis, and which has been described in various reptiles as the pterygoideus internus. It is completely homologous with the pterygoideus internus of the Caecilians.

The Pterygoideus internus muscle arises by an exceedingly strong band of tendon from the posterior surface of the os transversum, the descending process of this and the os pterygoideum, and from the margin of the last bone between the process and the articulation with the epipterygoid bone. This band widens rapidly as it passes back, forming a strong tendinous investment for the ventral and lateral surfaces of the muscle. Its lateral edge is much thickened and winds round the ventral edge of the mandible caudad, ventrad, and laterad, vertically below the coronoid process, without becoming bound to the mandible. A few of the most anterior and superior of the fibres of the muscle arise directly from the posterior surface of the descending process of the os pterygoideum above the origin of the tendon ; the whole of the rest arise from the upper surface of the tendinous sheathing. They are inserted on to both inner and outer surfaces and ventral edge of the mandible. On the outer side there is no insertion in front of the joint, but internally the insertion commences immediately behind Meckel's fossa. The fibres thus inserted are intimately fused with those of the pars anterior, and those inserted into the inner surface of the mandible behind them are in similar relation to the pars medius. Behind the joint facet the mandible is almost entirely enswathed by the muscle, only the extreme tip, where the depressor mandibulae is inserted, not being so covered.

There yet remains for description a portion of this muscle which must act as a depressor of the lower jaw, Depressor mandibulae mandibularis. These fibres arise from the posterior surface of the quadrate along the superior margin of the articular surface, actually from the upper part of the joint capsule. They pass directly back to be inserted into the superior edge of the mandible in front of the insertion of the (hyoid) depressor mandibulae. On the inner side the origin of these fibres is continued ventrad and rostrad on to the inner surface of the posterior arm of the os pterygoideum and they gradually assume a more vertical direction as their point of insertion is also carried forward along the mandible, and ultimately they are merged with the posterior portion of the temporo-massetericus muscle.

Innervation.—The whole of the muscles of mastication are innervated by branches of the R. mandibularis V which leave the nerve close to the ganglion. That to the pterygoideus internus runs down parallel and very close to the main inferior mandibular branch and internal to it. Just before the main nerve enters Meckel's fossa this motor nerve turns caudad and mediad. It is a nerve of some size and was traced back through the muscle for a considerable distance.

The Pterygo-quadratus muscle arises from a fine, but very strong, ligament which is attached above to the skull immediately below the incisura prootica and below to the pterygoid bone immediately behind the articular facet for the lower end of the epipterygoid. This ligament lies medially to and parallel with the epipterygoid. This muscle also arises from the lower edge of that flange of the prootic bone which forms the upper part of the lateral wall of the tympanic recess. This latter origin is confined to a very short length of the edge below and behind the incisura prootica. The fibres pass caudad, parallel to the posterior process of the pterygoid bone, and are inserted on the upper edge and inner surface of that process. The insertion extends back to the capsule of the pterygo-quadrate articulation.

Innervation.—This is by a twig from the Vth nerve, given off from the infero-posterior surface before the nerve breaks up into its three main rami.

No trace was found of a separate Spheno-pterygoideus muscle, though it was sought for in several specimens.

The function of this muscle is difficult to understand; both at its origin and insertion it is attached to rigid structures. The ligament of origin forms the lateral margin of the anterior aperture of the eustachian canal, but it does not seem that contraction of the muscle could affect the size of the aperture. The inner surface of the muscle in its upper one-third is covered by the tympanic mucosa, but as the muscle is straight from origin to insertion its contraction cannot change the size of the tympanic chamber.

THE DEVELOPMENT OF THE MUSCLES OF THE MANDIBULAR SEGMENT.

(Fig. 132.)

At stage 15 the ventral constrictor sheet is represented by a band of muscle fibres which extend along the middle third of the length of the short flexed Meckel's cartilage. These arise on each side from the periosteum of the cartilage and pass directly towards the mid-line, but do not reach their antimeres; a gap nearly one-quarter of the distance between the two cartilages is left between the muscles. The separation of this sheet into deep and superficial layers is apparent in places only; for the rest it appears as a single layer.

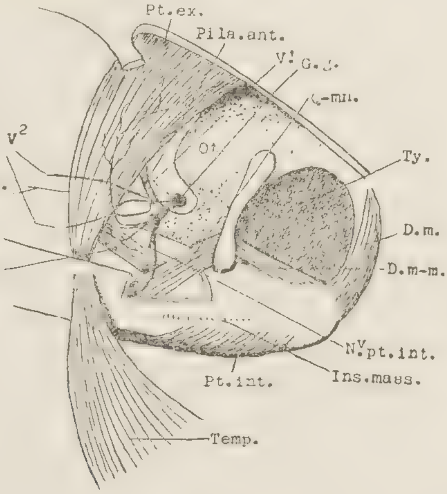


Fig. 132.—*Physignathus* embryo, stage 80.

At Stage 20 the sheet is a little longer antero-posteriorly, the fibres reach nearer the mid-line, and the separation into two layers has taken place completely. The deeper layer extends a little anteriorly to the superficial but does not extend quite so far back.

At stage 50 the superficial sheet extends back almost to the posterior end of the cartilage and it is to be noted that its origin throughout is from the cartilage. At this stage the origin of the muscle is perforated by the thyro-mandibularis in four places. The pterygoideus internus lies still entirely above the ramus of the jaw and to its inner side.

At 73 the pterygoideus internus has extended round below and laterally to the jaw and now is inserted on to the outer surface of the angular and surangular, and it has pushed the origin of the intermandibularis up on to the outer surface of the surangular and articular above it.

At 100 these two parts of the Csv.1 muscle are as in the adult.

The development of the adductor muscles of the lower jaw is particularly interesting, in as much as the later stages indicate very clearly the influence of the amphibian ancestry.

At 20 the primordium of these muscles consists of a "V"-shaped, exceedingly cellular, faintly striated and somewhat gelatinous mass of tissue. The point of the "V" is at the base of the ascending process of the palato-quadrate but lateral thereto. One arm extends dorsad and caudad behind the gasserian ganglion and the R. mandibularis V, and this is the larger arm. The other extends directly dorsad in front of the above nerve and ganglion but deep to the R. maxillaris V. It was quite impossible by dissection to demonstrate that the upper end of either arm was definitely attached. The posterior arm at its upper end lay upon the otic capsule; the anterior reached up to the taenia marginata in front of the capsule.

It is possible that a swelling seen on the anterior edge of the anterior arm was the primordium of the depressor palpebrae inferioris. This suggestion arises from the fact that it is assumed that the muscle in question is one of the mandibular muscles because it is innervated by the Vth nerve. I have been unable to find any stage in which the muscle was distinctly connected to the other muscles of the segment.

The insertion of the base of the two arms was into the perichondrium of Meckel's cartilage at the point where the coronoid process subsequently develops.

At 35 the muscles had increased in size and there was found a projection from the antero-lateral and ventral end of the anterior portion. This extends back some little distance between the posterior end of Meckel's cartilage and the posterior end of the palato-quadrate; it does not reach the cartilage of the lower jaw, but appears to end freely. This is the primordium of the pterygoideus internus, and its development is very much as Edgeworth (1931) describes the development of the muscle in *Sphenodon*.

The actual derivation of the several very definite components of the adult musculature, which are found in later stages, is exceedingly difficult to follow. The complete separation of the muscles by the rami of the fifth nerve, however, permits one to assert with a high degree of confidence that the three pterygoid muscles and the depressor mandibulae mandibularis are developed from the anterior arm and the rest of the muscles from the posterior.

At stage 80 (Fig. 132) there are no less than eight quite distinct muscles developed, most of which are already indicated at 50.

The Retractor Anguli Oris is a small muscle, relatively, just as in the adult.

The Masseter is exposed by the removal of the last muscle. This is a flat sheet of muscle which arises from the lower margin of the supratemporal arch just in front of the tympanum, and passes ventrad with an inclination rostrad, to be inserted on to the outer surface of surangular above the upper margin of the pterygoideus internus. This muscle is very readily demonstrable. One detaches the insertion and the whole sheet peels off the subjacent temporalis without the derangement of a single fibre on the contiguous faces of the two muscles.

The outer surface of the Temporalis is exposed by the removal of the masseter. Removal of the posterior boundary of the orbit exposes the anterior margin of the temporalis muscle, and the maxillary nerve may then be seen entering the orbit from beneath the margin. Using the nerve as a guide, the fibres are turned back and the muscle gradually detached from its origin. When the gasserian ganglion is exposed, the deep surface of the muscle is reached, and, turning this outward, the detachment of the muscle is completed. It is now seen that the muscle arises from the upper portion of the inner surface of the supratemporal arch, both surfaces of the posterior process of the parietal bone, the outer surface of the upper part of the otic capsule, and the upper part of the anterior surface of the quadrate. It is further found that, where the muscle is in contact with the pterygoideus externus in front, the two separate quite cleanly, and that at no other place is there any fusion between the deep surface of this and any subjacent muscle. When the temporalis is thus reflected outward and forward its two, relatively large, motor nerves are put on the stretch and brought very plainly into view. They leave the R. mandibularis V just distal to its emergence from the ganglion. The muscle is inserted on to the inner surface of the surangular, above Meckel's fossa.

The Quadrato-mandibularis is a quite separated little group of short muscle fibres which arise from the lower end of the quadrate across the anterior surface just above the articular end, and run forward and ventrad to be inserted along the top of the mandible and down each side a little way a short distance in front of the joint.

The Pterygoideus Externus arises from the posterior surface of the post-orbital bar, from the lower edge of the anterior end of the posterior process of the parietal, and from the greater part of the length of the epipterygoid bone. The fibres are inserted into a tendon within the depth of the muscle, and the lower end of the tendon is inserted into the tip of the coronoid and into the inner surface of the coronoid bone, in front of Meckel's fossa.

The most anterior fibres of the temporalis are inserted into this same tendon, in a manner precisely similar to that observed in the Urodele, *Necturus*.

The Pterygoideus Medius is a small muscle which arises from the outer surface of the posterior process of the pterygoid bone and is inserted into the articular bone below Meckel's fossa. This muscle is almost in contact with the quadrato-mandibularis posteriorly, but a small gap separates their margins.

The Pterygoideus Internus arises from the os transversum and pterygoid bone as in the adult, and is inserted into the articular bone below the insertion of the pterygoideus medius and also, on the outer side of the mandible, into the articular, angular and posterior portion of the surangular below the insertions of the Mm. massetericus, quadrato-mandibularis, depressor mandibulae mandibularis and depressor mandibulae muscles. The whole of the fibres of the muscle are horizontal in direction, almost at right angles with the other muscles.

The Depressor Mandibulae Mandibularis is quite distinct from the surrounding muscles. It arises from the upper margin of the posterior wall of the Q.-M. joint capsule and passes back to be inserted into the dorsal edge of the post-articular process of the mandible in front of the insertion of the depressor mandibulae. In its proximal half this muscle lies in the floor of the tympanic cavity, and this half may be clearly seen through the transparent tympanic membrane after the removal of the skin covering that membrane. This muscle may well be the precursor of the M. depressor mandibulae of the Monotremes.

THE COURSE AND RELATIONS OF THE RAMI OF THE FIFTH NERVE.

The Gasserian ganglion lies upon the outer surface of the membrana spheno-obturatoria immediately in front of the otic capsule. Apparently only two rami leave this ganglion, but it actually lies in a pocket of the dura which is extruded through the incisura prootica, and the R. ophthalmicus profundus turns inward and runs forward on the inner surface of the membrana spheno-obturatoria quite a distance before perforating it to enter the orbit.

The R. maxillaris leaves the anterior surface of the ganglion, carrying a short diverticulum of the dura with it. After a very short course laterad and rostrad against the posterior surface of the pterygoideus externus, it perforates the diverticulum and bears a ganglion. From the distal side of the ganglion two branches spring. One turns ventrad and rostrad, the other rostrad, both passing externally to the M. pterygoideus externus.

The nerve to the M. depressor palpebrae inferioris leaves the anterior surface of the gasserian ganglion distal to the R. maxillaris and runs forward deep to the M. pterygoideus externus.

Immediately the R. mandibularis emerges from the dural sheath, the two nerves to the M. temporalis are given off from the dorso-medial surface of the nerve, then the nerve to the M. pterygoideus externus leaves the anterior surface ; and at the same level, from the posterior face, the nerve to the M. pterygoideus medius is given off. The main ramus now continues ventrad against the deep surface of the M. temporalis, and a branch, apparently sensory, is given off which perforates the Mm. temporalis and massetericus and reaches the subdermal tissues of the lips at the angle of the mouth. Immediately after this the large nerve to the M. pterygoideus internus is given off from the ventro-medial surface and thereafter the main nerve enters Meckel's fossa. Its further course has been described as far as the departure of the anterior mylo-hyoid and the lingual nerves. These, it will be remembered, did not pass beneath Meckel's cartilage as did the mylo-hyoid nerve itself. After the two anterior nerves are given off the main nerve continues on its way along the upper edge of Meckel's cartilage within the mandible, diminishing as each of three more branches perforate the inner wall of the canal, and the terminal branch escapes in similar manner.

THE MUSCLES OF THE HYOID SEGMENT.

(Figs. 130–131.)

The Superficial Constrictor (Csd.2 and Csv.2) is continuous from the mid-dorsal to the mid-ventral line. The origin is from the dorsal intermuscular septum commencing just behind the transverse level of the posterior margin of the M. pterygoideus internus and extending thence for a distance equal to about one-third of the antero-posterior length of the head. The insertion, slightly wider than the origin, is into the mid-ventral raphe. The anterior fibres are parallel to the posterior fibres of the pars extramandibularis of Csv.1b, but are separated from them by a definite interval. Dorsally these fibres are similarly separated from the pars notognathica.

Innervation.—The anterior fibres are innervated by a small branch from the seventh nerve, which reaches the deep surface of the muscle behind the posterior margin of the pars notognathica. The greater part of the muscle is innervated by two nerves which come from the first two spinal nerves. The ventral rami of these two nerves join below the exit of the second, without, as far as I can see, giving off any branches. The compound nerve passes laterally and ventrally between the lower margin of the median and superior margin of the ventral trunk muscles ; it then turns laterad and appears behind the posterior-superior margin of the sterno-cleido mastoid muscle and immediately breaks up into several branches. One of the largest of these reaches the deep surface of the Cs.2 and again divides into three or four branches. Two of the larger of these penetrate the muscle and are probably sensory nerves. The remainder terminate in the muscle itself. Experimental work reveals that the spinal nerves do not supply motor fibres to the muscle.

The Depressor Mandibulae presents partes cephalognathica and notognathica very similar to those parts of the muscle in the Anura.

The Pars Cephalognathica arises from a small area of the squamosal and from the perimysium of the M. temporo-massetericus above and behind the tympanum. From this origin the fasciculi pass ventrad and caudad to be inserted into the post-articular process of the mandible in front of the insertion of the pars notognathica and above the insertion of the M. pterygoideus internus, and behind that of the depressor mandibulae mandibularis muscle. The area of origin is relatively small and all the fasciculi pass uninterruptedly from origin to insertion, except for a few posterior fibres which are fused with those of the pars notognathica just above the mandible.

The Pars Notognathica is similar to the pars cephalognathica but is larger ; it arises from a short length of the edge of the posterior process of the parietal bone close to the body of the bone, from a small pit lateral to that for the ligamentum nuchae (dorsal intermuscular septum) on the back of the body of the parietal, and from a short length of the dorsal intermuscular septum just behind this. The direction of the muscle is ventrad, caudad and slightly laterad, to its insertion on to the extreme dorso-posterior tip of the post-articular process of the mandible.

Superiorly the posterior corner of the M. temporo-massetericus lies between the two parts of this muscle ; inferiorly they are side by side.

Innervation.—This is by separate branches of the VIIth nerve which reach the muscle on its deep surface.

THE MUSCLES OF THE BRANCHIAL SEGMENTS.

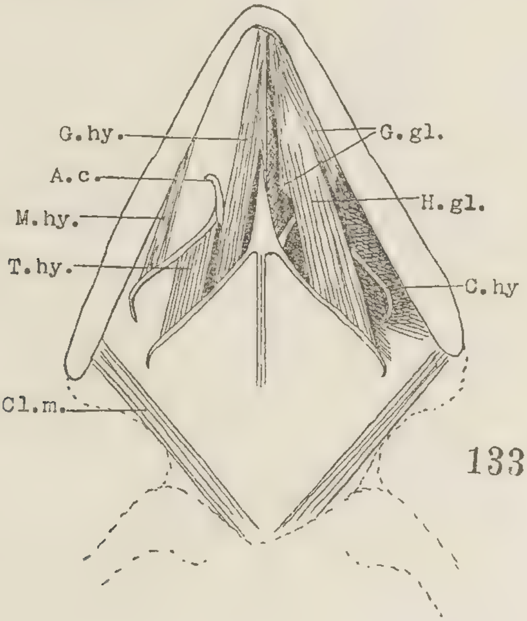
(Figs. 133, 134.)

THE HYPOBRANCHIAL SPINAL MUSCLES.

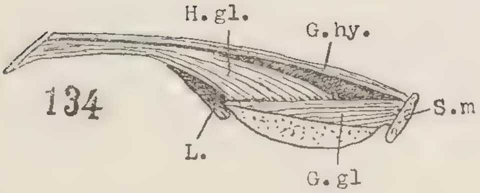
The Hyoid skeleton consists of (1) a median and anterior pars entoglossus of fibrocartilage, (2) a urohyal, also of fibrocartilage and double throughout its length, (3) paired slender hypohyals which are firmly attached, not jointed, to the median elements where urohyal and pars entoglossus join, and whose direction is laterad and rostrad from their origin, so that their distal ends come to lie close to the inner surface of the mandible a little in front of the middle of its length, (4) paired stylohyals attached by fibrous tissues to the distal end of the hypohyal and extending thence caudad nearly parallel to the ramus of the jaw, (5) paired thyrohyals which are articulated to the median elements immediately behind the attachment of the hypohyal and pass caudad and laterad, with a sinuous curve concave outward first and then concave inward, to terminate a little in front of the transverse level of the posterior end of the mandible and a short distance medially thereto.

In the adult lizard, when the superficial constrictors have been removed from the neck, and ventral to the hyoid skeleton, there appears to be a single, relatively thick, sheet of muscle arising from the clavicle, episternum and antero-ventral margin of the epicoracoid and passing thence to be inserted along the posterior edge of the thyroid cartilage. When, however, in the emergent embryo (stage 100) the muscle is freed from its origin, commencing at the lateral margin, a lateral and superficial portion of the sheet may be peeled from the rest without breaking any intermingled fibres. It is now found that in such juvenile specimens there are three separate sterno-thyroid muscles and, moreover, it is found that these three muscles may be demonstrated in the adult.*

The Sterno-thyroideus Lateralis muscle arises from the ventro-medial edge of the epicoracoid and from the episternum and clavicle for the greater part of the length of the latter. This origin is in part by the intermediation of the connective tissues superficial to the pectoral girdle and in part directly from the clavicle itself. The origin of the sterno-mastoid muscle is superficial to the medial portion of the origin.



133



134

Figs. 133-134.—*Physignathus.* Fig. 133. The deeper ventral muscles. Fig. 134. Median section of the tongue and floor of the mouth.

The insertion is into the posterior edge of the thyroid cartilage along almost its full length.

The Sterno-thyroideus Medialis is a narrow strip of muscle which arises from the clavicle and episternum to one side of the mid-line and passes forward to be inserted into the base of the urohyal and a very short length of the thyrohyoid cartilage alongside of it.

These muscles are placed so closely side by side that, in the adult no line of separation is obvious. The origin of the sterno-mastoid muscle is placed superficially to the contiguous margins.

---

* Although partly fused there can be no doubt that these three muscles are the same as those more completely defined muscles found in this situation in *Varanus* and other reptiles.

The medial muscle and portion of the lateral muscle are visible between the two sterno-mastoid muscles and behind the posterior margin of the Csv.2, whilst the posterior end of the lateral muscle is visible lateral to the sterno-mastoid and behind the Csv.2 when the skin is removed.

The Sterno-thyroideus profundus muscle is a thin sheet of fibres which arise from the anterior margin of the clavicle along its median two-thirds under cover of the origin of the above superficial muscles. From this origin the fibres pass rostrad, the lateral fibres with a laterad inclination, to be inserted along the posterior edge of the thyroid cartilage under cover of the origin of the same muscles. In the adult it is difficult to separate the superficial and deep muscles, but in the emergent embryo and slightly earlier developmental stages there is a definite difference in the direction of the more lateral fibres. Those of the superficial muscle have a slight inclination mediad from behind, whilst those of the deep muscle are inclined laterad. The deep muscle lies against the ventral surface of the trachea along its median edge and below the mucosa of the pharynx laterally.

The Thyro-mandibularis muscle arises from the lateral three-quarters of the length of the anterior edge of the thyroid cartilage and is inserted into the inferior edge of the mandible in front of the M. pterygoideus internus and into the outer surface of the mandible between this muscle and the portion of the M. temporo-massetericus, under cover of the insertion of the Csv.1b. Anteriorly, as already mentioned, this muscle perforates the Csv.1b in three of four slips to gain its insertion.

The Genio-hyoideus is placed on the same plane and lies medially to the thyro-mandibularis muscle. The origin is from the medial one-quarter of the anterior edge of the thyroid cartilage. Quite separate from its fellow of the opposite side at its origin, the muscle inclines towards the mid-line and about half-way forward of its length becomes fused with its fellow, the two being inserted together by a short narrow tendon into the back of the symphysis menti.

The Hyo-glossus muscle is a flat muscle which arises, under cover of the last two muscles, from the greater part of the length of the same, anterior, edge of the thyroid cartilage. It runs forward superficially to the thyro-hyoideus, as far as the stylo-hyal and then turns dorsad to end in the tissues of the tongue, reaching far forward.

The Thyro-hyoideus muscle arises from the same edge of the same cartilage under cover of the hyoglossus and passes rostrad to be inserted into the posterior edge of the stylohyal. This is a thin flat muscle.

The Hyo-mandibularis muscle arises from the inner edge of the mandible in company with the insertion of two of the perforating slips of the thyro-mandibularis, and passes caudad to be inserted into the anterior edge of the stylohyal laterally to the insertion, on the posterior edge, of the thyro-hyoideus muscle. The slips of origin of this muscle perforate the Csv.1b in the same manner as the slips of origin of the thyro-mandibularis muscle.

The Genio-glossus arises from the anterior end of the inner surface of the mandible, and its fasciculi pass caudad and dorsad at varying angles to be inserted into the tissues of the tongue. The greater part of these are inserted laterally to the hyoglossus muscle but a large minority are inserted medially to that muscle, which thus, as it were, splits this muscle into partes medialis and lateralis.

Amphibolurus.

This is an agamid lizard, allied to *Physignathus.* As was anticipated, its musculature is essentially similar to that just described. The only point of difference worthy of note is that the M. sterno-thyroideus profundus is very completely differentiated from the superficial muscle laterally. Its median fibres run directly antero-posteriorly and are fused with the deep surface of the medial superficial muscle. The rest of the fibres incline more and more laterad till the most lateral pass almost directly laterad. This lateral direction is made possible by the greater posterior extension of the thyroid cartilage. The lateral limit of the origin of the sterno-thyroideus lateralis lies deep to the insertion of the anterior fibres of the M. trapezius.

Anolis.

Anolis is one of the Iguanidae. I have for study seven specimens of the genus ; three each of *A. carolinensis* and *A. cristatellus,* and one of an unnamed species. They are all so closely similar that no differences worthy of note were observed.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1 presents superficial and deep portions as in the agamid lizards and, as in those, the superficial is divisible into intermandibular and extramandibular portions.

The muscles of mastication are intermediate in their state of differentiation between that of the adult and young *Physignathus*, and in addition one other muscle is present.

The Retractor Anguli Oris muscle is as in the Agamidae.

The Mm. temporalis, massetericus and quadrato-mandibularis are very completely fused.

The Depressor mandibulae mandibularis is not recognizable.

The three pterygoid muscles are well differentiated. The M. pterygoideus externus and internus are essentially as in the young *Physignathus*, the pterygoideus medius rises higher on the anterior portion of the otic capsule than in that form.

The Pterygo-quadratus muscle is a small triangular sheet of fibres which arises by its broader end from the posterior edge of the processus pterygoideus and from the skull immediately below the incisura prootica and extends horizontally caudad and slightly laterad to be inserted into the infero-medial corner of the quadrate. This muscle lies along the outer side of the eustachian passage and may well be the forerunner of the tensor tympani muscle of the mammals.

Innervation.—This is by a twig from the Vth nerve given off before that breaks up into its component rami.

The Spheno-pterygoideus muscle is a fine round strand of fasciculi which arise from the skull above the incisura prootica and pass directly ventrad to be inserted into the pterygoid bone immediately posterior to the articular facet for the epipterygoid bone.

Innervation.—This is by a twig from the ramus mandibularis V which leaves the nerve very close to its departure from the ganglion.*

MUSCLES OF THE HYOID SEGMENT.

The Csv.2 is essentially as in the Agamidae, but the peculiar posterior prolongation of the urohyal passes superficially to the muscle, issuing from beneath the posterior margin of the pars extramandibularis of the Csv.1b.

The Depressor Mandibulae is not divided into partes noto- and cephalo-gnathica; the origin of the muscle from the mid-dorsal intermuscular septum extends back almost to the anterior edge of the epicoracoid. The most posterior fibres run forward superficially to the pterygoideus and to the Csv.1b and terminate in a membrane which gives them insertion into the outer surface of the mandible in front of the M. pterygoideus internus.

The Hypobranchial Spinal muscles are essentially similar to those of the Agamidae.

Basiliscus.

This is another of the Iguanidae. It is a much larger lizard than the species of *Anolis*, but unfortunately I have only the head and part of the neck of a single specimen. This is perfectly preserved, and permits me to describe with confidence as much of the muscles as are present, but the absence of the anterior end of the pectoral girdle renders the account somewhat incomplete. So far as the material permits, one is enabled to say that there is a very close resemblance to the smaller iguanids just described. The urohyal, however, is not prolonged posteriorly and does not become superficial to the Csv.2.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a (M. submentalis) is continued right forward to the symphysis menti; anteriorly its fibres are directly transverse, but not araphic; further back they incline caudad and mediad beneath the anterior portion of the Csv.1b, M. intermandibularis.

The muscles of mastication are essentially similar to those of *Anolis*, the anterior fibres of the pterygoideus medius being fused with the deep fibres of the pterygoideus externus. This last muscle is remarkably developed. The parietal bone is produced backwards into a large laterally compressed supra- and post-occipital crest. From the side of this crest the pterygoideus externus muscle gains an additional area of origin, so that it projects back beyond the skull proper and high above the general contour of the head.

---

* There is little doubt that these two muscles represent the spheno-pterygo-quadratus mentioned by Edgeworth (1931, p. 804). It is, however, quite erroneous to describe them as a single muscle in the Iguanidae; their fibres are almost at right angles to one another.

THE MUSCLES OF THE HYOID SEGMENT.

As in *Anolis*, the Csv.2 is somewhat more extensive than in *Physignathus*.

The Depressor Mandibulae is smaller than that of *Anolis* ; its origin does not extend nearly so far caudad along the mid-dorsal line.

Actually the whole of the dorsal origin of the muscle, that from the mid-dorsal septum, lies under cover of the posterior extension of the pterygoideus externus muscle. The mid-dorsal septum actually extends forward to the usual terminal point at the back of the parietal bone ventrally to, and attached to, the ventral edge of the supra-occipital crest. It is not possible to recognize any division of the muscle into partes noto- and cephalo-gnathica, nor are any of the fibres inserted elsewhere than into the postarticular process of the mandible.

The Hypobranchial Spinal muscles are essentially as in *Physignathus*.

Chameleon.

(Fig. 135.)

Of this genus I have a single perfectly preserved specimen of *C. etienni*, from the Belgian Congo.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a (M. submentalis) is small, as in *Physignathus*.

The Csv.1b is represented by the pars intermandibularis only. The muscle arises from fairly high up on the inner surface of the mandible. Its posterior margin is just in front of the anterior end of the pterygoideus internus muscle as that curls around the lower edge of the mandible. The muscle is not perforated by any slips of the hypobranchial spinal muscles.

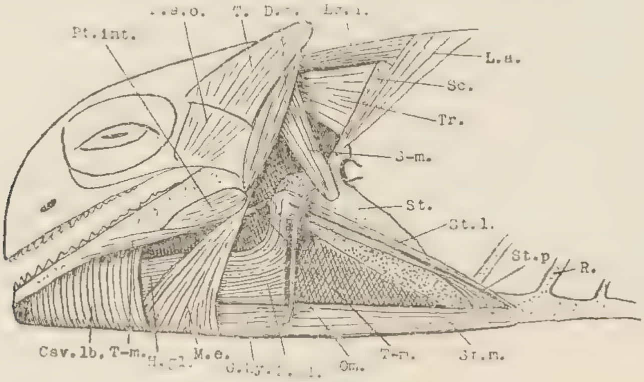


Fig. 135.—*Chameleon.*

The muscles of mastication are essentially as in the Agamidae. The occipital crest in *Chameleon* is more complex than that of *Basiliscus*. The median element is formed mainly from the parietal, but in part also from the supraoccipital, and there is, on each side, a supporting flying buttress formed by a posterior prolongation from the squamosal bone. The muscle that fills all the space between the components of the crest on each side is, not the pterygoideus externus (which is actually reduced in size), but the temporo-massetericus.

Pterygo-quadratus and Spheno-pterygoideus muscles are not definable.

THE MUSCLES OF THE HYOID SEGMENT.

The post-cephalic constrictor sheet (Cs.2) appears to be divided into two portions. Behind the depressor mandibulae there is a relatively broad, and exceedingly thin, diaphanous sheet of fibres which arise from the dorsal septum and pass right to the mid-ventral line. This sheet appears to be innervated only by fine twigs from a branch of the VIIth nerve which reaches the muscle from beneath the posterior margin of the reduced depressor mandibulae. Behind this diaphanous sheet is a second. This arises as a narrow band of fibres from the subdermal surface of the coracoid just behind the insertion of the M. trapezius. After a very short course ventrad, this band of fasciculi widens out, the fasciculi becoming separated, and this diverging of the fibres is continued to the mid-ventral line where they form a relatively broad sheet in front of the pectoral girdle.

The innervation of this posterior sheet appears to be entirely by fine twigs from the first two spinal nerves.

This is possibly a constrictor colli spinalis, portion of the panniculus carnosis, similar to that of the Chelodina.

The Depressor mandibulae is quite a small muscle. It arises from the back of the quadrate and from the postero-inferior edge of the "flying buttress" formed by the squamosal. There is no trace of any division of the muscle into two parts.

Innervation is by the VIIth nerve.

Musculus interhyoideus arises from the perimysium on the lower part of the posterior surface of the depressor mandibulae. At its origin the fibres of the muscle are gathered into a flat strand which passes ventrad behind the depressor mandibulae, then ventrad and rostrad behind and partly under cover of the pterygoideus internus, and finally ventrad and mediad. As soon as the fibres pass from beneath the last muscle they begin to spread out till, at the mid-ventral raphe, into which they are inserted, they form a tolerably wide superficial sheet. The posterior margin of this sheet lies in the transverse plane of the origin of the muscle, that is, at the posterior margin of the depressor mandibulae, the anterior fibres incline forward to be inserted into the median raphe deep to the posterior fibres of the Csv.1b pars intermandibularis.

Innervation.—This is by a fine branch from the VIIth nerve which curls around the posterior edge of the depressor mandibulae muscle to reach it.

One cannot but draw attention to the remarkable similarity of this muscle to the median portion of the pars interhyoidea of the elasmobranchian Csv.2, and its general similarity to the anterior portion of the Csv.2 of the amphibians. The origin, of course, is different from both of these. The origin of the muscle is strongly suggestive of that of the missing Csv.1b pars extramandibularis, but the situation of the anterior fibres mid-ventrally, deep to the pars intermandibularis, is not that of the anterior fibres of the pars extramandibularis in other lacertilians. The resemblance of this muscle to the M. interhyoideus in other reptiles confirms its identification.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The Hyoid Skeleton is peculiar, and like the muscles to be described next, it is apparently modified in association with the remarkable protrusible tongue.

The pars entoglossus, as in other lizards, is a fibro-cartilaginous structure. It is here peculiar in that it is not tapered but is of the same thickness from end to end. The posterior end of the entoglossal part joins the short hyaline cartilaginous body of the hyoid. To this latter a short cerato- and slightly longer thyro-hyal are articulated. The former extends laterad and dorsad towards the ramus of the jaw a short distance in front of the joint. No trace of a separate, or any, stylohyal was found. The thyrohyal is also a relatively short rod of cartilage ; its direction from the body of the hyoid is laterad and dorsad, with a very slight inclination caudad to terminate immediately behind the posterior end of the mandible, almost in contact with the insertion of the depressor mandibulae and pterygoideus internus. Both pairs of hyoid processes form incomplete half-hoops which conform to the contour of the deep throat at the root of the remarkable sheath of the tongue. These two half-hoops are very close together at the mid-line, where the processes are articulated to the hyoid body, but diverge slightly as they depart from their origin.

The Sterno-thyroideus lateralis arises from the mid-line of the sternum between the first and second sternal ribs. The muscle is a narrow ribbon of no great thickness, and it passes rostrad and laterad to be inserted into the extreme tip of the thyroid cartilage.

The Sterno-thyroideus medialis arises from the sternum just behind the origin of the M. sternothyroideus lateralis. This also is a relatively narrow ribbon, but somewhat thicker than the last muscle. It passes directly rostrad, alongside of its fellow, to be inserted into the root of the thyroid cartilage and back of the body of the hyoid. Its outer margin is strengthened by a tendinous strand which, continued rostrad past the hyoid, gives origin to some of the lateral fibres of the M. genio-hyoideus.

The Sterno-thyroideus profundus arises from the mid-line of the sternum for a short distance in front of the sterno-thyroideus lateralis. It is very similar to the last muscle and runs forward under cover of it to be inserted into the end of the thyroid cartilage.

The Omo-hyoideus muscle has not been found in any other lizard examined. It arises from the epicoracoid under cover of the insertion of the M. sterno-mastoideus. This is a very narrow and thin strand of fibres which passes nearly transversely, but with an inclination rostrad, superficially to the three sterno-thyroid muscles, to be inserted into the back of the body of the hyoid.

The Hyoglossus muscle arises from the greater part of the length of the ventral surface and anterior edge of the thyroid cartilage and passes forward to be inserted into the mandible far forward, on each side of the symphysis and under cover of the Csv.1. The fibres which arise farthest out, at and near the end of the cartilage, have a direction mediad and only slightly rostrad, until they join, and become bound up with, the more medial fibres, when they turn forward.

The Genio-hyoideus muscle arises from the symphysis menti and passes rostrad alongside of its fellow, and medially to the last muscle, to be inserted into the inner end of the thyroid cartilage.

The Thyro-mandibularis muscle is a narrow ribbon of fibres which arises from the extreme end of the thyroid cartilage and passes forward under cover of the " swelling " of the pterygoideus internus muscle. In front of this last muscle the thyro-mandibularis becomes superficial to the posterior margin of the Csv.1b, and its membranous tendon is continued forward some distance before finally being inserted along the lower edge of the mandible.

The Thyro-hyoideus muscle arises from the anterior edge of the thyroid cartilage and is inserted into the posterior edge of the ceratohyal. The direction of the fibres is from their origin mediad with an inclination rostrad. This muscle is blended with the deep surface of the hyo-glossus.

No Hyomandibularis muscle was found.

The Genio-glossus muscle arises from the symphysis menti and runs back along the side of the sheath of the tongue for the greater part of the length thereof. A little in front of the hyoid body the muscle turns dorsad and is inserted into a median raphe on the dorsal surface of the sheath between the body of the hyoid and the posterior end of the larynx.

In comparing the above description with that of Lubosch, it will be noted that I find a thyro-mandibularis in the situation of the branchio-mandibularis visceralis of this author. I have not been able to find the branch of the IX nerve to this muscle. Lubosch has failed, in his specimen, to find the interhyoideus muscle but has found a deep, dorsal, part of the Csv.1 in, nearly, the situation of the interhyoideus (Lubosch, Fig. 9, C_2 mv.dors.).

Geckos.

(Fig. 136.)

Two genera of Geckos have been dissected, several specimens of *Gymnodactylus phyllurus* and one of an unnamed species of *Thecadactylus*. They are almost identically similar in their musculature.

Particular interest attaches to the ventral musculature.

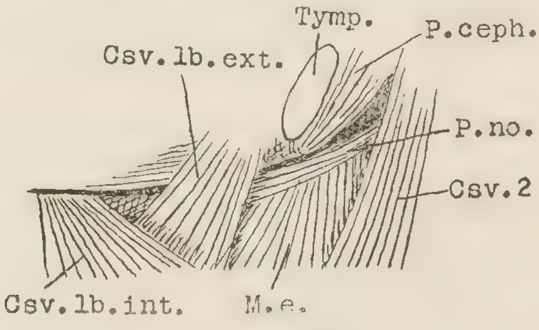


Fig. 136.—Gecko.

The two portions of the Csv.1b are quite separate. The pars intermandibularis arises from a little less than the middle one-third of the mandible, and its fibres radiate, the anterior mediad and the posterior caudad. The separated pars extramandibularis rises from the perimysium of the pterygoideus internus and its fibres trend mediad and rostrad, forming an angle with the posterior fibres of the pars intermandibularis.

The Interhyoideus muscle arises, deep to the pars cephalognathica of the depressor mandibulae, from the internal, vertical edge of the quadrate near the dorsal end of the bone. The fibres trend mediad, radiating so as to produce a relatively wide band of muscle at the mid-line. As the muscle passes from beneath the post-articular portion of the mandible, they pass deep to the anterior end of the pars notognathica of the depressor mandibulae.

Innervation.—This is, as in *Chameleon*, by a branch of the VIIth nerve which reaches it from beneath the depressor mandibulae muscle. This innervation would seem very definitely to indicate that the muscle must be regarded as a deeply situated portion of the hyoid constrictor.

The Pars cephalognathica of the depressor mandibulae is as in the generality of lacertilians.

The Pars notognathica is peculiar. It arises from the dorsal intermuscular septum under cover of the hyoid constrictor sheet. The insertion is not into the post-articular portion of the jaw ; the fibres pass forward ventrally and medially to the angle of the jaw and become lost in the connective tissue deep to the pars extramandibularis of the Csv.1b.

The post-cephalic hyoid constrictor fibres are essentially similar to the whole of the Cs.2 in *Physignathus*.

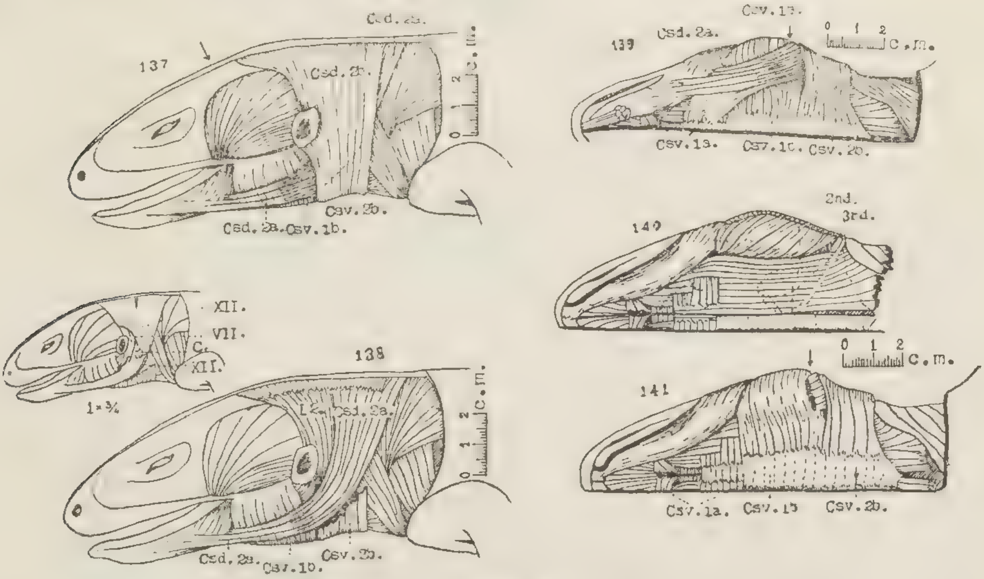
The muscles of mastication may be briefly dealt with. There is no retractor anguli oris recognizable, the M. pterygoideus is small, no depressor mandibulae mandibularis is recognizable. The M. pterygo-quadratus and the M. spheno-pterygoideus are present.

The hypobranchial spinal muscles are essentially as in typical lacertilians, except that a complete transverse tendinous inscription interrupts the continuity of the lateral and medial sterno-thyroid muscles, and these two are not definable, one from the other.

Tiliqua.

(Figs. 137–141, from Lightoller.)

Tiliqua is one of the genera of the Scincidae. I have been able to dissect, also, two other members of the family, both belonging to the genus *Lygosoma*. They are all essentially alike. Lightoller has described most of the cephalic muscles of *Tiliqua scincoides*, and for the most part they are similar to those forms already described.



Figs. 137-141.—*Tiliqua* (from Lightoller).

The M. submentalis (Scv.1a) is represented by small triangular sheet of fibres which arise by a fine tendon from the median surface of the mandible close to the symphysis menti. The fasciculi trend caudad and mediad and are inserted into a median raphe. The posterior end of the muscle lies deep to the anterior end of the pars superficialis of the same muscle.

The Pars notognathica of the depressor mandibulae resembles that muscle in Iguanidae in that it is not inserted into the mandible, but is continued forward to be inserted into the superficial fascia on the ventrum of the mouth, and by this medium becomes attached to the lower margin of the mandible anterior to the extramandibular portion of the Csv.1b. The origin of this portion of the depressor lies deep to the Csd.2, but anteriorly the muscle lies superficially to the pars extramandibularis of the Csv.1b.

The muscles of mastication are more completely fused than in any other lacertilian studied. There is recognizable only the division into temporo-masseteric and pterygoid portions as described by Lightoller.

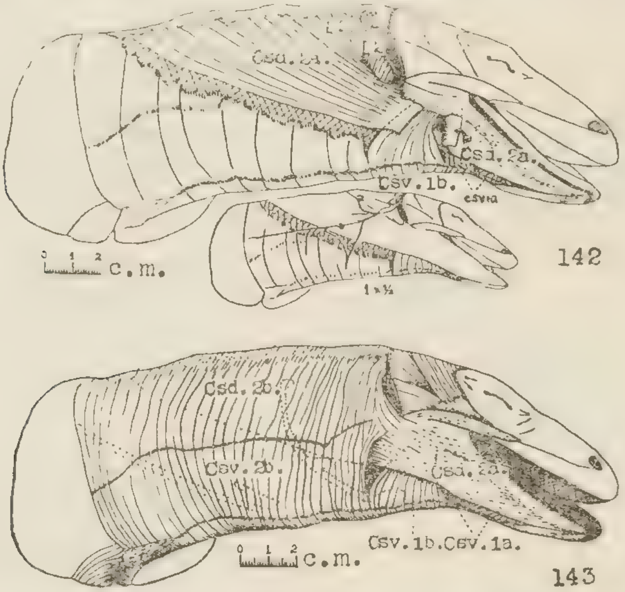
The hypobranchial spinal muscles are similar to those of *Physignathus.*

Varanus.

(Figs. 142–143, from Lightoller, 144–147, from Bradley.)

The superficial constrictor muscles of *Varanus varius* have been described by Lightoller and the muscles of mastication of *V. bivittatus* by Bradley.

Lightoller's description of the superficial muscles is complete and accurate and I have reproduced his drawings.* It should be noted, however, that he includes the M. submentalis and the M. intermandibularis of the ventral mandibular constrictor as portion of the Csv.1a, whilst I regard the latter as being portion of the Csv.1b. This difference of interpretation arises from the fact that in none of the reptiles dissected by Lightoller was the M. submentalis developed as a distinctly separated muscle such as is present in *Physignathus,* and many other reptiles.



Figs. 142-143.—*Varanus* (from Lightoller).

I find that the anterior portion of the Cs.2, both dorsally and ventrally, is innervated by the VIIth nerve as Lightoller describes, but I find that the greater part of the muscle is innervated, like that of *Physignathus,* by the conjoined first and second spinal nerves. Here again experimental work reveals the absence of motor fibres to the muscle in the spinal nerves.

Bradley's description of the muscles of mastication of *V. bivittatus* might almost serve as a description of those of *V. varius.* The retractor anguli oris, indicated by Bradley, is quite readily dissected off the subjacent M. temporo-massetericus (capiti-mandibularis of Bradley). The Mm. pterygo-quadrate and spheno-pterygoideus (Mm. pterygo-sphenoidalis posterior and pterygo-parietalis of Bradley) are essentially similar to those muscles in *Anolis.*

---

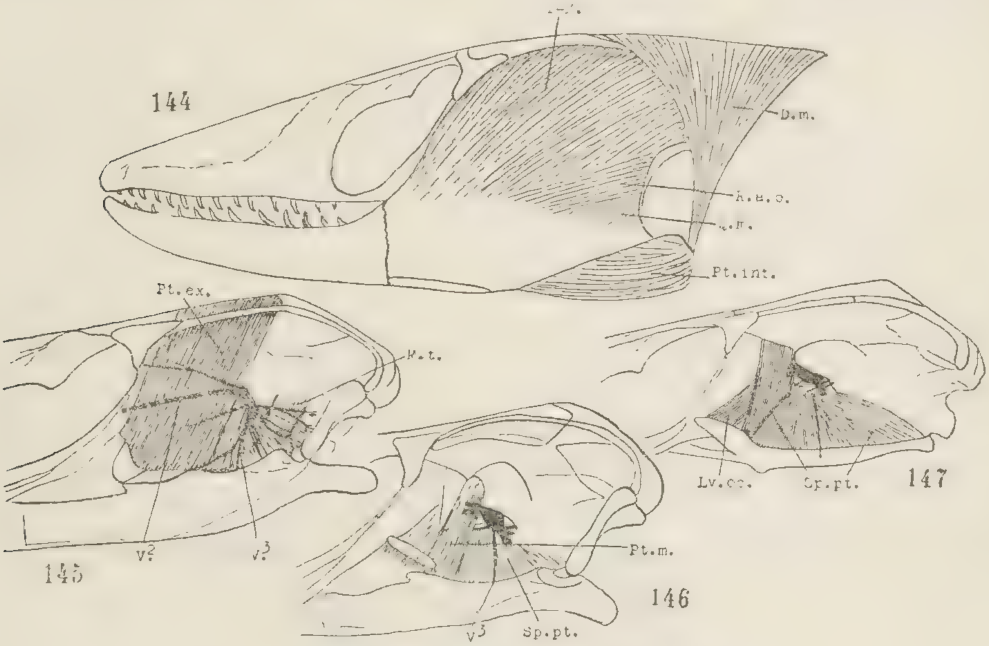
* This has been made possible by his kindness in giving me advance proofs for the purpose, and I have to thank him for the same assistance with the illustrations of *Sphenodon.*

2. Rhynchocephalia.

(Figs. 148–149, from Lightoller.)

Sphenodon is, of course, the only recent representative of this group. Osawa (1898), Lubosch (1933), and Lightoller (1935) have described the cephalic muscles. I reproduce illustrations from Lightoller.

The superficial ventral constrictor muscles are, in my specimens, very similar to those in his. In my specimens, however, the partly separated posterior slip of the Csv.1b which arises under cover of the depressor mandibulae (Csv.1b¹ of Lightoller, Vb of Lubosch), is quite distinctly continuous with the more deeply placed " M. interhyoideus " of Lightoller's description. This latter muscle is undoubtedly the homologue of that which I have described in *Chameleon* and other lacertilians as the M. interhyoideus. I find that in the specimen of *Sphenodon* which I have dissected it is not difficult to free the origin of the muscle from the stylohyoid bone, and that when this is done it is found that a fascial sheet carries the origin of the muscle up to the posterior edge of the quadrate. One might therefore describe the muscle as having this last origin, and as being bound to the stylohyal as it passes over it.



Figs. 144-147.—*Varanus* (from Bradley).

This is the first reptile I have dissected in which no trace of the M. submentalis (Csv.1a) could be found.

Whilst the form of the superficial ventral constrictors in my specimen is very much as described by Lightoller, differing only in that the posterior, shorter portion is rather more extensive, I find that the innervation is as described by Lubosch. I therefore agree with the latter that the Csv.1b of Lightoller's description is the anterior portion of the Csv.2 ; herein *Sphenodon* resembles Crocodiles.

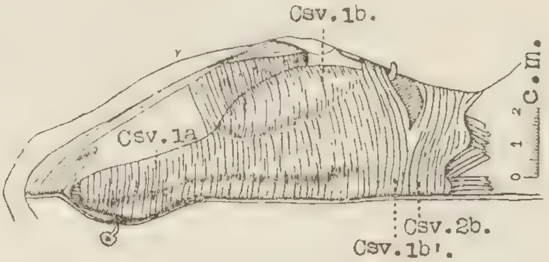
Immediately after the VIIth nerve leaves the tympanic cavity, as described by Lightoller, it divides into four branches. Three of these pass directly into the overlying Depressor mandibulae, the fourth and largest branch runs ventrad against the deep surface of that muscle, passes through the origin of the M. interhyoideus from the stylohyal cartilage, and reaches the deep surface of the last-mentioned muscle. It then breaks up into very fine branches. The most anterior of these to be detected, passes directly mediad along the M. interhyoideus. No branch of this was observed to reach the anterior margin of the muscle. The rest of the branches of the nerve pass caudad on the deep surface of the Csv.2.

I would agree with Lightoller that the Csv.1 is innervated only by the Vth nerve, but must agree with Osawa and Lubosch that the interhyoideus and the Csv.2 are innervated by the VIIth.

I find, moreover, that the posterior, shorter, fasciculi of the Csv.2 are very definitely innervated by a twig from the ventral ramus of the second spinal nerve. The main nerve issues from between the dorsal and ventral trunk muscles a little anteriorly to the anterior margin of this posterior portion of the Csv.2. The twig to the muscle turns caudad and ventrad around the upper margin of the cleido-mastoid muscle, and terminates by breaking up on its deep surface. Whether the second cervical nerve anastomoses with the first was not determined by actual observation, but in as much as that the nerve to the M. cleido-mastoid was observed to leave the emergent main trunk, it is confidently believed to do so. Material has not been available for experimental work, but the results in the lacertilian examples suggest very emphatically that the spinal innervation of the muscles is sensory only.

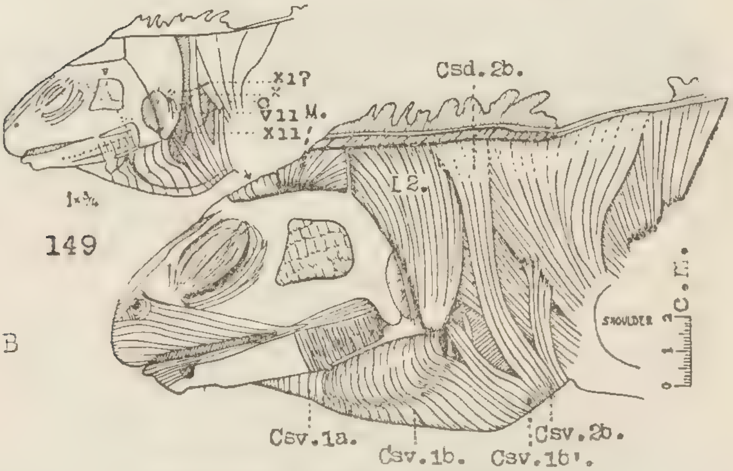
A

148



149

B



Figs. 148-149.—*Sphenodon* (from Lightoller).

The Depressor mandibulae muscle is precisely as described by Lightoller. The absence of the pars notognathica is peculiar, but not unique; its absence has been noted in *Chameleon*, and in *Anolis* the muscle, though extensive, is not divided into two portions.

The Retractor anguli oris muscle appears to have been overlooked by previous workers. It is possible that the ease with which I was able to detach the bones of the facial arcades after they had been decalcified, together with my practice of staining my dissection subjects, permitted me to find a small muscle which others had missed. The muscle arises from the deep surface of the jugal bone along its length, and also from the deep surface of the post-orbital bone at the level of the upper margin of the posterior ramus of that bone.

The insertion is into the tissues of the upper lip.

This muscle is a triangular sheet of fibres, quite thin posteriorly, where the fibres have a direction ventrad and rostrad. Anteriorly the muscle becomes thicker, and that portion arising high up behind the orbit passes down between the eye and the temporalis muscle as a definite rounded strand of fibres which increase in bulk and spread out in the longitudinal plane, before reaching the corner of the mouth, as they descend ventrad to their insertion.

The innervation is by a fine twig, presumably of the fifth nerve, which perforates the temporo-massetericus muscle about the middle of its antero-posterior length and a short distance above the upper margin of the jugal bone.

The muscles of mastication are as described by Lightoller and Osawa, and in this respect *Sphenodon* is very similar to *Physignathus*. There is a further resemblance to that lizard in the form and situation of the M. pterygo-quadratus (Spheno-pterygo-quadratus of Edgeworth, 1931). The muscle is well developed and it differs from that of *Physignathus* only in that the fibres trend more ventrad to their insertion.

The Pterygo-mandibularis of Edgeworth is the pterygoideus internus of this work. That of *Sphenodon* differs from that of *Physignathus* only in that its origin is continued rostrad along the dorsal surface of the pterygoid bone anteriorly to the os transversum.

The remaining cephalic muscles of *Sphenodon* are so essentially lacertilian in character that they do not call for detailed description.

3. Crocodilia.

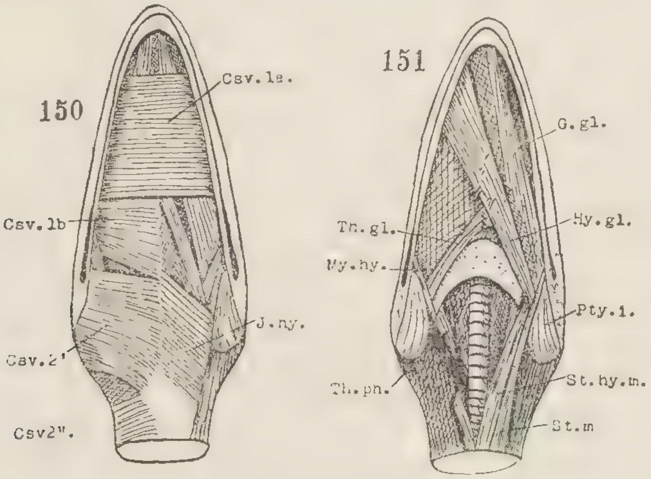
(Figs. 150–151.)

Material.—The following account of the cephalic musculature is based upon the dissection of two specimens of Alligator. These are but recently hatched young; the larger measures 4 cm. from tip of snout to occiput, the other is a few millimetres shorter, both are, unfortunately, cut off in front of the shoulder girdle.

MUSCLES OF THE MANDIBULAR SEGMENT.

Csv.1.—The small size of my material made it quite impossible to determine with confidence the innervation of most of the muscles, and this difficulty arose in connection with the ventral constrictor sheets. There is a very clear definition of these sheets into four parts. It is believed that the first two only are mandibular.

Csv.1a—The Submentalis.—A relatively extensive sheet of araphic fibres is thus identified. It is composed of transverse fibres which are quite continuous from side to side. They arise from the inner surface of the mandible along a line which is closer to the dorsal than the ventral edge. This line commences a short distance behind the mentum and ends a little way behind the middle of the length of the lower jaw.



Figs. 150-151.—Alligator.

Csv.1b—The Intermandibularis.—The origin is from a similar line along the mandible immediately behind the Csv.1a, but only about half as long. These fibres have a direction slightly caudad; they are inserted into a median raphe, many of them cross the mid-line and form a narrow strip of latticed fibres.

No Retractor anguli oris was found.

The Temporo-massetericus muscle is not so massive as was the general rule in the Lacertilia.

Origin is from the outer part of the ventral surface of the quadrate, and from the ventral surface of the quadrato-jugal and jugal as far forward as the suture with the os transversum.

Insertion is on to the inner surface of the surangular along the posterior half of its length.

The Pterygoideus externus muscle presents the usual clean face of contact with the more superficial temporo-massetericus muscle, with the ramus maxillaris trigemini lying upon it between the two muscles.

Origin is from the inferior surface of the extreme upper end of the quadrate, from the whole of the bones surrounding the supra-temporal fossa and from the adjacent ventro-posterior surface of the alisphenoid.

Insertion : The fibres arising from the supratemporal fossa curve rostrad and ventrad, the rest of them pass directly ventrad, all with a slope laterad, to be inserted on to the inner surface of the surangular in front of the insertion of the temporo-massetericus.

Pterygoideus medius has an extensive origin from the greater part of the inferior surface of the quadrate, from the inferior surface of the alisphenoid, and from the ascending lamina of the pterygoid bone.

Insertion : The fibres pass ventrad and laterad to be inserted into the surface of the angular which bounds the fenestra in the mandible.

Pterygoideus internus.—Origin is from the edges and contiguous area of the upper surfaces of the bones surrounding the palatal vacuity, and from the anterior bony margin of the intorbital vacuity.

Insertion : The fibres pass caudad and ventrad to be inserted on to the inner surface of the angular in front of the insertion of the pterygoideus medius.

Pterygoideus inferior (Pty.i.).—This is a massive group of fibres which bulges subdermally medial to posterior end of the jaw.

Origin : This is from the upper surface of a strong fascial membrane which is attached to the posterior edge of the palatal lamina of the pterygoid bone.

Insertion : The fibres pass caudad and slightly ventrad, and then dorsad to be inserted into the inferior surface of the angular behind the joint. The most dorsally placed of these fibres lie immediately below the lowest fibres of the pterygoideus medius muscle, namely, those arising from the lower part of the ascending lamina of the pterygoid bone ; the two sets of fibres are at right angles to one another, and they separate leaving clean faces to the muscle. These superior fibres of the pterygoideus inferior pass almost directly rostrad to their insertion on to the angular.

Pterygoideus anterior.—This is a small bundle of fibres which appear to be quite separate from the rest of the complex pterygoid muscle. They arise by a very strong fibrous membrane from the lower edge of a meniscus of cartilage which is attached to the lateral edge of the palatine lamina of the pterygoid bone.

Insertion : The little brush of fibres passes directly ventrad to be inserted on to the inner surface of the dentary bone in front of the fenestra in the lower jaw, and, where the laminate suture permits, the surangular to extend forward on the outer surface of the hinder end of the dentary.

Innervation of the muscles of the mandibular segment.—Branches of the ramus mandibularis have been observed innervating all parts of the muscles of mastication except the last. The usual innervation of the anterior portion of the ventral constrictor, by twigs from the main nerve as it courses along Meckel's canal, was observed also. It was not possible to trace any of these last on to the intermandibularis muscle, nor was any other possible course of innervation observed.

Discussion.

The identification of the submentalis rests upon the complete absence of the median raphe. Throughout the Amphibia and in certain of the cartilaginous and bony fishes there was observed an anterior ventral mandibular constrictor which differed from the rest of that sheet in the absence of a median raphe. Though, in those forms, the muscle in question lies always, as far as at present known, close behind the mentum and differs from the muscle in the Alligator in that it is a relatively thick muscle, still it is believed that the very distinctive feature which characterizes this muscle so constantly in those other vertebrates justifies the present identification.

The Muscles of mastication resemble closely those of the Lacertilia. The separation of the lower portion of the pterygoideus internus, forming the pterygoideus inferior, may be regarded as a direct concomitant with the extreme posterior transportation of the jaw articulation.

The absence of any pars extramandibularis in the crocodilian Csv.1 is of interest. Even if that muscle which I have identified as the Csv.2′ (pars anterior) be in its anterior portion innervated by the Vth nerve, and this I regard as being extremely unlikely, it is still not extramandibular in its origin. It certainly resembles the pars extramandibularis of many lacertilian forms in that it covers the portion of the pterygoid muscle which, in those forms, is inserted on the outer surface of the jaw. The correlation of the absence of the pars extramandibularis and of any insertion for the pterygoideus upon the outer surface of the mandible is of interest. It will be remembered that the extramandibular origin of the constrictor sheet in the lacertilians was regarded as being a secondary condition brought about by the growth of the pterygoid muscle outside the jaw, and as not being of phylogenetic significance. The conditions in the Alligator appear to support this view.

THE MUSCLES OF THE HYOID SEGMENT.

The Superficial Hyoid Constrictor sheet extends further forward than it does in the lacertilians or in *Sphenodon*. It is very distinctly divided into two portions.

The Pars anterior.—This arises for the most part from the inferior edge of the mandible (Fig. 150, Csv.2′), but in its posterior portion it arises from the ligamentum nuchae by a membranous extension. The fasciculi themselves do not extend dorsad above the level of the mandible. This muscle occupies the situation of that which Lightoller designates the pars extramandibularis of the Csv.1. It lies superficially to that portion of the complex pterygoid muscle which corresponds to the posterior end of the pterygoideus internus of the lacertilians, but in this reptile the insertion of either of the muscles does not extend on to the external surface of the mandible. The direction of the fibres is mediad and caudad. The anterior fibres are at an angle with the posterior fibres of the Csv.1b and are separated from them throughout their length. The insertions of the M. sterno-mandibularis and of the M. mylo-hyoideus lie in the gap between the Csv.1 and Csv.2′.

Insertion: This is into a median ventral raphe. The greater part of the fasciculi extend right to the mid-line, but posteriorly they fall short.

Pars posterior (Csv.2″).—This is a much smaller sheet of fibres which arise from the dense fibrous tissue which invests a group of subdermal cervical glands placed at the mid-lateral line of the neck in front of the shoulder girdle. Their direction is mediad and rostrad. The most anterior fibres do not reach the mid-line, the posterior do.

Insertion: Into a median raphe continuous with that of the pars anterior.

Innervation.—This is by a branch facial nerve.

The Interhyoideus muscle of the Alligator (I.hy.) is a remarkably well developed and extensive muscle. Its origin, however, is peculiar.

This is a sheet of fasciculi which lies immediately deep to the Csv.2 on either side of the mid-line, but which burrows very deeply for its attachment. The two muscles of either side together enclose the ventral capiti-nuchal muscles, the pharynx, the trachea, and the hypobranchial spinal muscles, in a tube which, however, is incomplete above, where the two ventral capiti-nuchal muscles lie on each side of the mid-line. The muscle extends from the posterior margin of the thyroid cartilage backwards for a distance of 1·5 mm. (The full length of the mandibles is 4·2 mm.)

Origin: This is from an intermuscular septum which separates the lateral and ventral capiti-nuchal muscles. The septum is quite short and the fasciculi of the interhyoideus extend up between these trunk muscles. A few of the most anterior fasciculi have an origin from a fine membrane which passes dorsad laterally to the lateral capiti-nuchal muscle and is attached above to the posterior edge of that lamina of the quadrate which covers the lateral surface of the exoccipital bone.

Insertion: The anterior fibres are inserted into a very short length of the posterior margin of the thyroid cartilage immediately below the trachea, the fibres behind these, about one-third of the full number, are inserted into a median raphe of their own, which lies in contact with the trachea. The rest of the fasciculi are inserted into the same raphe as the pars anterior of the Csv.2′.

From their origin the fasciculi pass ventrad. Posteriorly they lie first between the trunk muscles, then between the lateral trunk muscle on the outer side, and the pharynx, trachea and spinal hypobranchial muscles on the inner side. Anteriorly the same structures lie to the inner side, but the pterygoideus inferior lies to its outer side. It thus reaches the deep surface of the Csv.2′ and at once turns mediad to its insertion, superficial to all the structures which lie medial to it.

The Depressor Mandibulae.—This muscle appears to be divided into anterior and posterior parts when viewed upon the removal of the skin, but no plane of separation could be demonstrated.

Origin: From the lateral half of the postero-superior surface of the quadrate, the ridge of the squamosal above that, and then along the dorso-posterior edge of the parietal and supra-occipital to the mid-line, and finally back along the ligamentum nuchae for a short distance.

Insertion: The direction of the anterior fibres is caudo-ventrad and slightly laterad, that of the posterior fibres ventrad and laterad. They are all inserted on to the dorsal surface of the post-articular piece of the articular bone.

Innervation of the muscles of the hyoid segment.—These appear to be innervated only by the facial nerve. That nerve leaves the acoustico-trigeminal fossa by perforating the prootic bone in the roof of the fossa. It thus reaches the anterior wall of the tympanic cavity, it rises on this wall till it meets the anterior margin of the tympanum, and then turns back around the median margin of the tympanum, and at its posterior margin bends ventrad and enters a canal between the dorsal surface of the quadrate and the parotic process of the exoccipital, and which is enclosed immediately behind the tympanic cavity by the squamosal laterally and above, the exoccipital medially, and the quadrate below. The posterior aperture of this canal is about half-way down the shaft of the quadrate and just on the dorsal surface above the median edge. Immediately the nerve emerges from the canal it gives off three small twigs which enter the M. depressor mandibulae. They were not traced far into the muscle—one did well to find them at all—but were assumed to be entirely motor nerves to that muscle. The main nerve turns ventrad and mediad, running behind and slightly laterally to a vessel which accompanies it through the canal, and which is taken to be the vena capitis lateralis. In this situation the nerve lies against the upper and then the deep surface of the M. pterygoideus inferior. It thus reaches the anterior margin of the M. interhyoideus, and at once breaks up into fine branches. Of these, three small ones break up upon the lateral surface of the muscle. The largest branch runs ventrad parallel with the fasciculi of the muscle till the under surface of the Csv.2′ is reached, and on this surface its branches trend both back and forward and terminate. The other branch of size passes caudad along the lateral surface of the M. interhyoideus, between it and the lateral trunk muscle, but trending ventrad.

There remains for description another muscle, probably hyoid. This may be provisionally designated the Depressor Auriculae. The tympanic recess in the Alligator is protected by a thick flap of skin. This is attached, along the dorso-median margin of the recess, to the squamosal bone and to the same bone along the upper half of the posterior margin. The flap is thickest behind, and in this thickened portion there is lodged a small pyramidal muscle. The base of the pyramid is muscular and is attached to the lateral surface of the squamosal bone near its posterior end. The apex of the pyramid is tendinous and is inserted into the quadrate at the postero-lateral margin of the tympanic recess. The obvious function of this interesting little muscle is to pull the tympanic covering flap close against the edge of the recess.

Discussion.

Passing from the lacertilian muscles to those of the Alligator, it was at once thought that the muscle which has just been designated Csv.2′ was the pars extramandibularis of the Csv.1. Its situation is exactly that which one would have anticipated for a pars extramandibularis. It would seem, however, that there can be little doubt that it is the homologue of the more posterior muscle. This seems to be quite conclusively proven by its innervation. It is true that in certain of the Elasmobranchs Lightoller observed an invasion of the Csv.1 by the VIIth nerve, but nowhere in the amphibians or in the lacertilians is there such an invasion. Osawa has stated that a branch of the facial nerve innervates the Csv.1 in *Sphenodon*, but, as already noted, Lightoller was unable to find such in his dissection, nor could I find any twigs of the VIIth nerve (supplying the Csv.2) running forward into the Csv.1 territory. In the present dissection it has been possible to demonstrate the innervation of this muscle by the VIIth beyond question, and in a manner very similar to the innervation of the Csv.2 not only in *Sphenodon* but also in the Lacertilians. There is, however, no trace discoverable of any innervation by spinal nerves in this reptile.

The manner of innervation of the Csv.2 is in itself distinctive, quite apart from the actual source of the nerve, when it is compared with the manner of innervation of the Csv.1. The hyoid muscle is innervated by a nerve which reaches its deep surface and spreads thereon, whilst the components of the Csv.1 are supplied with motor nerves upon their superficial surface.

The origin of the M. interhyoideus alone causes one to hesitate in so identifying this muscle in the Alligator. It is, however, significant that this peculiar origin is correlated with the complete loss of the wide-spreading hyoid cornua. Another little feature, perhaps not without its significance in this respect, is that there is a small anterior bundle of fasciculi of this muscle with an origin from the skull in close proximity to the upper end of the stylohyal. May it not be that the loss of the hyoid cornua has, in this reptile, caused the muscle to find a new point of origin, and that the last portion to do so was that attached to the tip of the stylohyal ? This, perhaps, became divorced from the cartilage when that was completely taken into the tympanic cavity. The attachment of part of the fasciculi to the same raphe as the Csv.2 recalls conditions observed in the Elasmobranchs.

The Depressor Mandibulae muscle calls for little comment. It were mere speculation to suggest whether or no the undivided muscle represents one of both the parts so often present in the Amphibians and Lacertilians.

It appears more than probable that the Depressor Auriculae is a separated portion of the depressor mandibulae, but as no trace of its innervation was found, this is not certain. Its situation, completely separated from the muscles of the mandibular segment, and almost continuous with the deep anterior border of the depressor, certainly points to its origin from that muscle.

In view of the fact that the depressor mandibulae has been regarded as the muscle from which the post-auricular muscles of the Mammalia are derived, it would be of interest to find it forming such a muscle in one of the reptiles.

The Hypobranchial Spinal Muscles.

The reduction in the hyoid apparatus appears to have been responsible for marked changes in the origins and insertions of these muscles as compared with their probable homologues in the Amphibia and Lacertilia. It is unfortunate that both my small specimens have been cut off in front of the shoulder girdle. I am, therefore, unable to determine the origin of those of these muscles which arise from the girdle.

The Sterno-thyroideus medialis (St.hy.m.) is inserted on to the little posterior wing of the thyroid cartilage.

The Sterno-mandibularis (St.m.) is probably the homologue of the sterno-thyroideus lateralis. It is inserted on to the inner surface of the mandible in the gap between the Csv.1 and Csv.2′. These are narrow thick strap-like muscles which taper from behind forward to their insertions.

The Hyomandibularis (My.hy.) muscle lies deep to the sterno-thyroideus. It arises from the tip of the posterior wing of the thyroid and is inserted on to the mandible just behind the overlying muscle.

The Hyo-glossus (Hy.gl.) muscle also arises from the wing of the thyroid cartilage by a short strong tendon. Passing forward, it broadens out and crosses the mid-line in front of the thyroid cartilage, and is inserted into the tissues of the tongue well forward along the lateral area thereof. As this muscle crosses the mid-line it interlaces with its antimere.

The Thyro-glossus (Th.gl.) appears to be a separated portion of the last muscle. It arises from the wing of the thyroid cartilage in front of the other muscles and, interdigitating with its antimere, is inserted into the tissues of the tongue around the anterior wall of the laryngeal depression. Its function is, fairly certainly, to pull the anterior wall of the depression against the posterior and to cover in completely the laryngeal opening.

The Genio-glossus (G.gl.) muscle arises from the inner surface of the mandible on either side of the mid-line and, passing back, its fibres spread out to be inserted into the tissues of the side of the floor of the mouth behind the insertion of the M. hyoglossus.

The Thyro-pharyngeus (Th.ph.) muscle arises from the dorsal edge of the posterior wing of the thyroid cartilage. Relatively broad at the origin, the fasciculi converge as they pass caudad and dorsad around the side of the pharynx to be inserted into the tissues thereof slightly dorsal to its mid-lateral line.

Crocodilus.

The Trustees of the Australian Museum presented me with a specimen of *Crocodilus* sp. about two feet long. The careful dissection of this specimen failed to disclose features wherein its cephalic musculature differed materially from that of the Alligator.

My thanks are tendered to Dr. C. Anderson, the former Director, and to the Trustees for the specimen.

The contribution of Lubosch on the visceral musculature of the Sauropsida reached me after my own work upon the Reptilia had been completed. When it was found that his description of a number of forms differed from my own, the dissections in question were either repeated or, having been preserved in sufficiently complete condition, the dissections already made were examined again.

Whether the marked difference between his description of the muscles of Alligator and my own are explainable as the differences between the young individuals and the adults I am not in a position to say, but that appears hardly possible. After going over the dissections again most carefully, I am unable to find that my original descriptions were at fault.

Outstanding among the differences is the fact that Lubosch failed altogether to find the remarkably well developed muscle which I have identified as the M. interhyoideus. The M. mylohyoideus of my description is very much more developed in the adult ; Lubosch identified it as the third constrictor (C.3, Fig. 30) and regards that which I have designated the M. thyropharyngeus as a deeper, more dorsal portion of the same muscle (Fig. 34).

It has not been possible to confirm the statement of Lubosch that these two muscles are innervated by the IX nerve ; on the other hand, it cannot be denied. " Failure to find ", in specimens so small as mine, cannot be relied upon as negative evidence.

4. The Chelonia.

Chelodina longicollis.

(Figs. 152–153.)

Material.—This reptile is quite common in the streams throughout New South Wales and I have been able to avail myself of a practically unlimited supply of adults. I have also had a number of specimens taken from the egg a little while before hatching.

MUSCLES OF THE MANDIBULAR SEGMENT.

The Intermandibularis muscle (Csv.1) shows no division into separate portions.* It arises from the inner surface of the mandible. Commencing in front, alongside of the symphysis, the line of origin is almost at the inferior margin ; as this line passes caudad it rises steadily and terminates, well toward the upper margin of the dentary, just in front of the insertion of the temporalis muscle. The whole of the fibres have a direction mediad and caudad.

Insertion : Anteriorly the fasciculi are inserted into the floor-plate of the mouth at some distance from the mid-line. Posteriorly they are inserted into a median raphe.

Innervation.—This is by three small branches of the mandibular ramus of the Vth nerve which perforate the mandible and spread over the superficial surface of the muscle.

The Temporalis muscle is by far the most massive component of the muscles of mastication. It arises from the dorso-lateral surface of the alisphenoid lamina of the parietal bone and from the whole of the dorsal surface of the depressed area of the skull behind and above the prootic foramen.

The insertion is into the upper edge and outer surface of the coronoid process of the mandible.

There is a fibro-cartilaginous meniscus attached to the inner edge of the upper surface of the coronoid process. This meniscus is folded down alongside of the coronoid process, between it and the upturned edge of the antero-lateral corner of the pterygoid bone. The lateral surface of the meniscus is lined by buccal mucosa and lies against a similar surface. Between it and the pterygoid bone there is a synovial cavity, the bone being covered with a layer of cartilage and that in turn by the synovial membrane.

The Pterygoideus externus lies entirely under cover of the M. temporalis. It arises from the anterior surface of the alisphenoid lamina of the parietal bone medial to, and in front of, the prootic foramen.

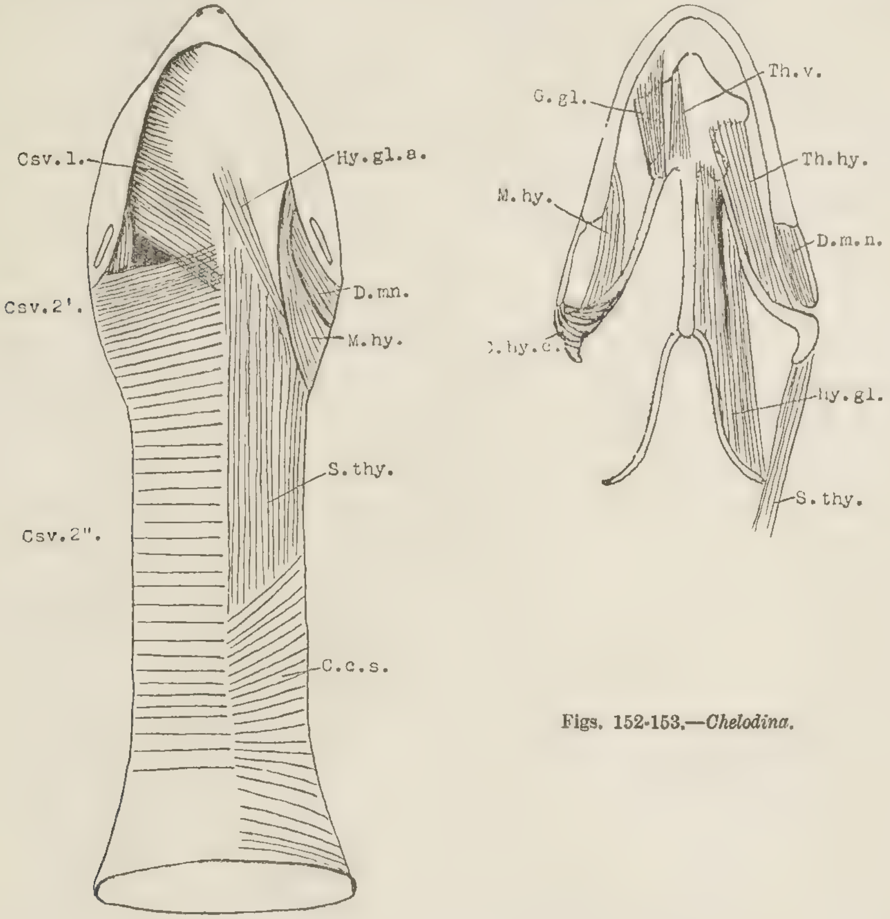
---

* In the late embryo there is a small submentalis muscle. This is a compact rounded bundle of fibres which pass from one ramus of the jaw to the other without any median raphe.

The insertion is into the articular bone very close to the inferior edge of the inner surface and well back just in front of the joint.

The muscle is crossed superficially, along its upper line of origin, by the maxillary ramus of the Vth nerve and below, just above its insertion, it is crossed diagonally by the mandibular ramus just before that reaches Meckel's fossa on the inner side of the mandible.

The Pterygoideus medius arises from the upper surface of the pterygoid bone laterally to and in front of the prootic foramen, behind the via masticatoria, and also from the anterior surface of the quadrate in front of and below the origin of the M. temporalis.



Figs. 152-153.—*Chelodina.*

The insertion is into the surangular bone above Meckel's foramen.

The Pterygoideus internus arises from the upper surface of the pterygoid bone in front of the via masticatoria.

The insertion is into the inner surface of the angular immediately in front of the insertion of the M. pterygoideus medius and below Meckel's fossa.

Innervation.—The muscles of mastication are innervated by branches of the ramus mandibularis V which leave the main nerve close to the gasserian ganglion.

MUSCLES OF THE HYOID SEGMENT.

The Hyoid superficial Constrictor Sheet is very definitely divided into two portions.

Pars anterior (Csv.2′).—The fibres arise from a membrane which is attached to the subdermal margin of the posterior bony wall of the tympanic cavity and supratympanic bulla, and then extends across the supratemporal trough, superficially to the posterior end of the temporalis muscle, to become attached to the crest of the supraoccipital, and is also attached for a short distance behind this to the ligamentum nuchae. The muscle fibres do not extend dorsad of the line of the jaw.

The insertion is into a median raphe. The direction of the fasciculi is mediad and rostrad and the first few pass beneath, deep to, the posterior fasciculi of the Csv.1.

Innervation.—By the two terminal branches of the motor division of the VIIth nerve.

Pars posterior (Constrictor Colli Spinalis*) (Csv.2″).—This muscle should, in all probability, not be described as one of the hyoid muscles. It is, however, included in this section because it is so closely similar to the posterior portion of the Csv.2 of other reptiles already described. Its separate identity was determined by stimulation experiments. These yielded a very definite boundary between this and the "constrictor colli facialis" in front. This is an extremely extensive sheet of muscle which extends, from just posterior to the jaw, back along almost the full length of the neck. It arises from the ligamentum nuchae for the anterior two-thirds of its length, and here the muscle fibres extend right round the neck from mid-dorsal to mid-ventral lines. The posterior one-third of the fasciculi arise from an intermuscular septum at the mid-lateral line. This line of origin is immediately below the tendon of the plastro-nuchal muscle. This tendon is attached by three digitations to the hinder ends of the lateral processes of the second, third, and fourth cervical vertebrae. The anterior limit of the mid-lateral line of origin of the constrictor colli spinalis is at the attachment of the posterior digitation.

The insertion is into a mid-ventral raphe.

Innervation.—This is by a strong branch from the united first and second spinal nerves. The ventral ramus (no dorsal ramus of the nerve was found) of the first spinal nerve runs backward below the longer dorsal trunk muscles and joins the second, apparently without giving off any branches. The ventral ramus of the second spinal nerve divides immediately after it issues from its foramen. These pass side by side, first caudad and ventrad, then ventrad, and finally rostrad and ventrad. The anterior of the two branches thus comes to meet and unite with the first spinal nerve. The conjoint nerve continues rostrad and reaches the deep surface of the constrictor colli spinalis from between the sterno-thyroideus and the cerato-hyoideus-capitis. It at once turns caudad and runs back along the deep surface of the neck so as to continue along the deep surface of the shorter posterior fasciculi of the muscle, giving off small twigs all the way, the nerve grows steadily finer and finer.

The Depressor Mandibulae presents no division into separate parts. It arises from the posterior surface of the squamosal where that bone forms the hinder wall of the supratympanic bulla.

The insertion is into the post-articular piece of the articular bone.

Innervation.—Two twigs from the motor division of the VIIth nerve.

The Interhyoideus muscle would probably not have been recognized as such had the adult Chelodina only been studied.

In the adult (Fig. 152, Hy.gl.a.) the muscle is a small triangular fan of fasciculi which arise from the median border of the ceratohyal immediately in front of the insertion of the lateral portion of the M. hyoglossus. The muscle lies against the deep surface of the Csv.2′.

The insertion is into the posterior edge of the floor plate of the mouth.

Innervation.—This is by a twig from one of the terminal branches of the motor division of the VIIth nerve. This leaves the deep surface of the Csv.2′ at the outer edge of the interhyoideus and breaks up upon the superficial surface of the muscle.

The true nature of this muscle was discovered in young specimens almost fully developed, taken from the eggs. In these, the muscle is inserted into the same median raphe as the Csv.2′. Its innervation was determined by separating the whole of the Csv.2′ together with the posterior portion of the Csv.1 and the anterior portion of Csv.2″ and the interhyoideus, and slicing off and detaching with them the superficial layers of the Mm. depressor mandibulae, ceratohyoideus-capitis and posterior end of the M. hyoglossus. These last three were then carefully dissected off the constrictor sheet from the deep side and the remainder of the preparation stained and mounted for examination under high magnification. The nerve could not be found in the adult.

---

* The muscle is a portion of the panniculus carnosus, but has been given this designation after much of my work on the Theria has been completed. A muscle which is deemed to be completely homologous with it is present in the Cetaceans, but, in them, extending very much further forward (Kesteven, 1941*d*). The reason for the introduction of this term is to emphasize the presence of a superficial constrictor innervated by spinal nerves as well as the facial constrictor. This, and the designation constrictor colli facialis, will be found in later sections of the work and used with the same intent.

THE COURSE AND MOTOR BRANCHES OF THE FACIAL NERVE.

Together with the Vth nerve the facial leaves the cranial cavity through the prootic foramen. In the trigemino-facialis fossa the facial lies above the trigeminal and the geniculate ganglion lies above the separated trunk of the trigeminal. From the ganglion the facial nerve swings laterad and then caudad through the prootic bone. Passing above the columella auris near its inner end, the nerve enters a short canal and appears on the base of the skull just below the posterior corner of the squamosal. In this situation it lies against the deep surface of the depressor mandibulae, and gives to that muscle two twigs. The nerve now divides into two branches and these turn dorsad and laterad around the posterior surface of this muscle, and reach the deep surface of the Csv.2′. Both the branches are distributed to the Csv.2′. None were observed to reach fibres of the Csv.2″ or to extend on to the Csv.1.

SPINAL MUSCLES.

The Constrictor Colli Spinalis Profundus.—This name is applied to a constrictor muscle not observed in any of the vertebrates previously dissected.

The muscle arises from the same intermuscular septum as do the short posterior fibres of the constrictor colli spinalis, but extends right back to the last cervical vertebra so that it here lies above the clavicle.

Insertion : The direction of the fibres is ventrad and mediad with a slope caudad in front and a slight inclination rostrad posteriorly.

Innervation.—By a branch of the ventral ramus of the third spinal nerve.

In the young specimens this muscle was found to be inserted, as to its anterior fasciculi, into the deep surface of the anterior margin of the plastron, and as to the rest of the fasciculi, into a strong facial sheet which is attached medio-ventrally to the plastron behind the first insertion and laterally to the scapula. This insertion suggests strongly that the muscle is really the cleido-mastoid, which otherwise is not developed.

THE HYPOBRANCHIAL SPINAL MUSCLES.

The larynx in this reptile has been brought right forward so that it lies in the floor of the mouth anterior to the middle of the length of the jaws. The forward migration of the larynx has, of course, been accompanied by the thyroid cartilage ; it has also resulted in the abolition of a fleshy tongue. It would appear that the latter has been replaced by a tough fibro-cartilaginous plate which lies ventrally to the thyroid cartilage, and which has been here designated the "floor plate". The thyroid cartilage has short anterior wings, to which, however, the ceratohyal is not attached. It is suggested that another of the results of the forward migration of the thyroid has been the transfer of the articulation of the ceratohyal to a more posterior situation. Posteriorly the thyroid is produced into a long median rod, and to the end of this the two posterior cornu are articulated.

The forward migration of the larynx and its cartilage has also, apparently, resulted in an arrangement of the hypobranchial spinal muscles which is very different from that of the Lacertilians. In the following description the designations adopted are those which reflect the homologies of these muscles with those of the Lacertilians, in so far as such are determined ; in some cases, however, the homologies have not been determined, even tentatively, and in these instances noncommital descriptive names are used.

The Genio-hyoideus (G.gl.).—This muscle lies deep to the floor plate, between it and the thyroid cartilage. It arises from the inner surface of the mandible to one side of the symphysis. The direction of its fibres is caudad and slightly mediad. They are inserted on to the posterior margin of the thyroid cartilage and on to the perimysium of the hyoglossus at its insertion.

The Hyo-glossus (Hy.gl.) arises from the whole of the outer surface of the posterior cornu of the hyoid. It is incompletely divided into medial and lateral portions. The former is inserted into the posterior edge of the thyroid cartilage between the bases of the two cornua. The lateral part is inserted into the anterior one-third of the inner surface of the ceratohyal.

The M. genioglossus (Th.v.).—The muscle thus identified arises from the anterior edge of the hyoid cartilage. Its fasciculi run directly caudad and are inserted into the deep surface of the floor plate.

The thyro-hyoideus muscle (Th.hy.) is a thick rounded bundle of fasciculi which arise from the lateral surface of the greater part of the length of the ceratohyal and pass forward and slightly mediad to be inserted on to both ventral and dorsal surfaces of the anterior wing of the thyroid cartilage.

The Hyomandibularis (M.hy.) muscle arises posteriorly to the last muscle from the remainder of the lateral surface of the ceratohyal. The solid bundle of fibres pass forward to be inserted into the inner face of the mandible anterior to the joint.

The Cerato-hyoideus-capitis (C.hy.c.) muscle arises from the outer edge of the tip and from the anterior edge of the ventral surface of the lateral end of the ceratohyal and, passing dorsad and rostrad superficially to the outer end of the Mm. mylohyoideus and depressor mandibulae, is inserted on to the flange of the squamosal bone which stands out above and behind the supratympanic bulla.

The Sterno-thyroid (S.thy.) muscle arises from the dense subdermal fascia along a line which commences ventrally at the mid-line a little behind the middle of the length of the neck, and inclines forward as it rises dorsad to the mid-lateral line. It is a thin sheet of fasciculi which pass directly forward to be inserted, for the most part, into a membrane and tendon which attach it to the ventral surface of the thyroid and the perimysium of the muscles inserted thereon. A few of the more lateral fibres are inserted on to the outer end of the ceratohyal, and these are also firmly bound to the tip of the posterior cornu of the hyoid as they pass over it.

Innervation.—The very complete fusion of the hypoglossal with the vago-accessorius trunk renders it impossible to be confident as to the innervation of these muscles. It appears that the greater part of the hypoglossal fibres leave the fused trunk on its inner side shortly after the nerves emerge from their bony canals, but of this one cannot be certain. A further complication is introduced by the fact that branches from the two separate trunks join the other before the nerve to the hypobranchial spinal muscles separates from the rest of the resultant network.

The Glossopharyngeal nerve was dissected out and the branch to the larynx found to turn ventrad and mediad around the posterior margin of the ceratohyoideus-capitis, then to run forward along the median edge of the ceratohyal, and then to turn dorsad between the ceratohyal and the lateral margin of the hyoglossus posterior.

Emydura macquariae.

I am indebted to the Trustees of the Australian Museum for a specimen of this tortoise, and tender them my thanks.

The Submentalis muscle is quite clearly differentiated from the intermandibularis. It takes the form of a small sheet of fibres, continuous from side to side, situated deep to the anterior end of the M. intermaxillaris.

The M. interhyoideus is similar to that of the young *Chelodina.*

The M. constrictor colli spinalis profundus is not differentiated from the M. constrictor colli spinalis superficialis. There is a continuous sheet of fibres extending as far back as in *Chelodina,* but there is no overlapping of two sheets.

Apart from these differences the cephalic musculature of these two fresh-water Chelonians is essentially similar.

5. **Ophidia.**

(Figs. 154–156.)

Material.—A practically unlimited supply of specimens of two common snakes has permitted a very complete survey of the adult myology. The two are *Python variegatus* and *Pseudechis porphyriacus.* These resemble one another and published descriptions of other snakes so closely that it has been confidently assumed that there was no necessity to dissect any other species.

It has not been possible to study the development of the muscles. In serial sections, those of young *Notechis scutatus* were observed to present no marked differences from those of the adult species studied.

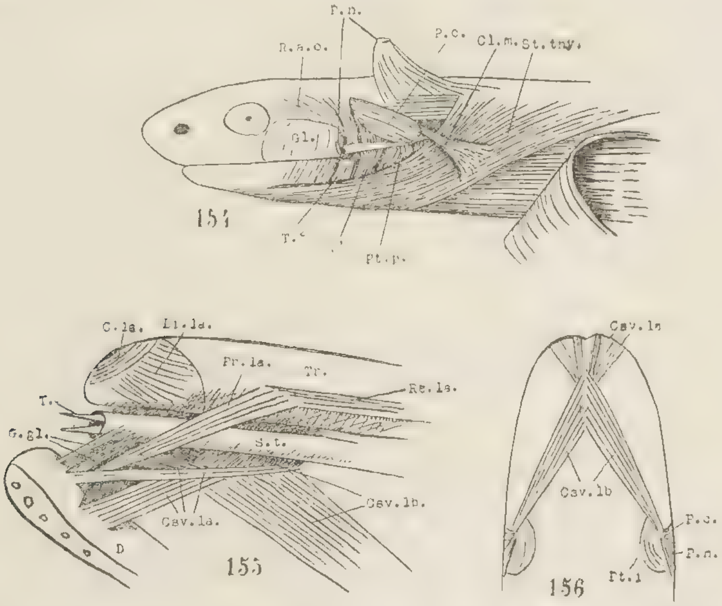
THE MUSCLES OF THE MANDIBULAR SEGMENT.

The ventral constrictor is sharply divided into anterior, submentalis, and posterior, intermandibularis, parts as in other reptiles.

The Submentalis (Csv.1a) resembles the pars profunda of the anterior portion of the mandibular constrictor of the Lacertilians.

In *Pseudechis* it consists of two portions, both of them quite small. The larger of these consists of a small quadrangular sheet of fibres which arise from the inner surface of the dentary close to the anterior end of the bone. The fasciculi pass caudad and mediad to be inserted into a median raphe which is placed above the submental crease, and which in its posterior part is common to this muscle and the Csv.1b, the latter being the more superficial of the two muscles. The smaller part of the muscle arises from the extreme tip of the dentary and passes caudad, dorsally to the fibres of the other part of the muscle, to be inserted into the same median raphe, but posteriorly to the other fibres.

In the *Python* the muscle is undivided and its fibres interlace with those of the Csv.1b at their insertion into the median raphe so that the two muscles appear to be continuous and interlacing at the mid-line. In fact it was thus that Hoffmann, following D'Alton, treated the conjoint Csv.1a and Csv.1b, designating them the intermaxillaris. Comparison with *Pseudechis* and the reptiles generally leaves no doubt that there are the two separate muscles blended at their insertions.



Figs. 154-156.—*Pseudechis*. T., tongue; T^1. & T^2., Mm. massetericus major and minor.

The Intermandibularis (Csv.1b) is similar in the two forms. It arises from the inner surface of the posterior end of the dentary and surangular, and also from an aponeurotic ribbon which is attached to the inferior margin of the tendon of the pars notognathica of the M. depressor mandibulae and to the inferior edge of the angular below the insertion of the pars cephalognathica of the same muscle. The fasciculi pass sharply forward, and gradually reach the mid-line, to be inserted into the median raphe already described in connection with the Csv.1a, and superficially to that muscle in *Pseudechis*, but interlacing with it in *Python*.

The dissections of Lubosch indicate a greater variation in the disposition and extent of the parts of this muscle, amongst the snakes, than might have been anticipated from the facts revealed in my two dissections. There is, however, a fundamental similitude in all the dissections.

MUSCLES OF MASTICATION.

These are exceedingly complex and their action has been studied by students of snake-bite. In the course of their studies they have described the anatomical form and relations of the muscles, but unfortunately these descriptions are, for the most part, given without any explanation of the nomenclature used as compared with that of other workers.

The latest of such works, and the most careful, is by N. H. Fairley (1929). I tabulate below his nomenclature, that of Hoffmann and the nomenclature of this work.

This work.	Hoffmann.	Fairley.
Retractor anguli oris	Parietali-quadrato-mandibularis, 1*a*	Anterior temporal muscle
Masseter minor	Not noted	Anterior temporal muscle, mandib. part
Masseter major	Par.-quadr. mand. 1*b*	Middle temporal muscle
Temporalis	Par.-quadr. mandib. 1*c*	Posterior temporal muscle
Pterygoideus externus	Par.-quadr.-mandib. 1*d*	?
Pterygoideus medius	Occipito-quadrato-mandibularis 2*b*	Pterygoideus internus
Pterygoideus internus	Transverso-maxillo-pterygo-mandibularis	Pterygoideus externus
Spheno-pterygoideus anterior	Pterygo-parietalis	Pterygo-palatine
Pterygo-quadratus	Pterygo-sphenoidalis posterior	Spheno-pterygoideus
Spheno-pterygoideus	Pterygo-sphenoidalis anterior	Parieto-pterygoideus
Median slip of the Spheno-pterygoideus	Vomero-sphenoideus	?

The Retractor Anguli Oris (R.a.o.) is a very extensive muscle. In *Python* it arises from the parietal and post-orbital bones just behind the orbit. The fasciculi pass ventrad and laterad, with an inclination caudad, to be inserted into the tissues of the lower lip immediately behind the angle of the mouth.

In *Pseudechis* the muscle is more extensive; its origin extends back along the parietal, and behind that bone the muscle arises from an aponeurosis superficial to the other muscles. The fibres pass ventrad and laterad, and are inserted into the dorsal and posterior margins of the capsule of the venom gland.

In both snakes there is a very strong quadrato-maxillary ligament which occupies, superficially to the muscles, the situation of a quadrato-jugal bone. This ligament crosses the tendinous lower end of the retractor anguli oris muscle in the Boidae and lies along the lower margin of the capsule of the venom gland in the Colubrine snakes.

Innervation.—This is by a branch of the mandibular ramus of the Vth nerve which leaves the main trunk soon after it emerges through its foramen in the side wall of the cranium, and reaches the muscle from beneath the anterior border of the Mm. temporalis and masseter.

The Masseter muscle is not differentiated from the temporalis in *Python variegatus*, but in *Pseudechis* one can recognize two portions, of the masseter and also the temporalis as quite separated muscles. Hoffmann's reproduction of D'Alton's illustrations of the muscles of *Python bivittatus* indicates that therein the entities of the masticatory muscle group are almost as well differentiated as in the colubrine snake *Pseudechis*.

Masseter minor (T^2).—This muscle arises from the deep surface of the retractor anguli oris. It is a relatively small muscle and its fibres pass directly ventrad to be inserted into the outer surface of the mandible.

Fairley describes this muscle as the mandibular slip of the anterior temporal muscle. That is to say, he regarded it as a partly separated portion of the retractor anguli oris. The insertion into the mandible, however, indicates quite definitely that it is not a portion of that muscle. Fairley failed to observe that the retractor anguli oris of the Boidae is not inserted into the mandible, and this explains the confusion.

Innervation.—This is by a branch of the mandibular ramus of the Vth nerve which leaves the main trunk along with all the other nerves to the muscles of mastication.

Masseter major (T^1).—This muscle has an aponeurotic origin from the supraoccipital bone. It is a fairly massive muscle and its fibres pass ventrad and laterad to be inserted into the upper edge and outer surface of the surangular.

The Temporalis muscle is larger and thicker than the more superficial masseters. It arises from the lateral, descending, plate of the parietal, and its fibres are inserted into the upper edge of the surangular, medial to the insertion of the masseter minor muscle.

Innervation.—By a branch of the mandibular ramus of the Vth nerve which breaks up into several smaller twigs as it enters the muscle.

The foregoing description of the Mm. masseter minor, masseter major and temporalis is based upon the muscles of *Pseudechis*. In *Python variegatus* there is a temporo-masseteric mass of muscle which arises from the area of origin of the three muscles in *Pseudechis*, but in which the three components are but poorly indicated by superficial depressions and intervening membranous partitions from both sides of which the fasciculi arise.

The Pterygoideus externus.—This is a quite small muscle which takes its origin from the anterior end of the lateral plate of the parietal bone, and from there its fibres pass ventrad deep to the maxillary ramus of the Vth nerve to be inserted into the lower edge of the internal surface of the angular. In *Python* the muscle is reduced to a thin ribbon of fasciculi, which, moreover, are of a dark grey colour, recalling the degenerating muscles of the developing tadpole.

Innervation.—By a branch from the ramus mandibularis similar to that innervating the other muscles.

Pterygoideus medius.—This muscle is reduced in both of the snakes studied ; that is, reduced when compared with the muscle in other reptiles. In *Pseudechis* the muscle is still separated from the pterygoideus internus, but in *Python* it is completely fused therewith.

The muscle arises from the posterior end of the pterygoid bone and its fibres pass caudad and laterad to be inserted into the inner surface of the angular behind Meckel's foramen.

The Pterygoideus internus (Pt.p.) muscle arises from the anterior end of the os transversum by a very strong, rounded, tendon. The muscle rapidly swells into a thick rounded mass of fibres which pass back beneath the mandible, to be inserted on to its inferior surface below the joint.

Innervation.—In *Pseudechis* the nerve to the M. pterygoideus internus passes down between it and the pterygoideus medius, that to the latter muscle leaving the other at the superior margins of the two.

The Spheno-pterygoideus anterior is very similar in the two snakes. It arises from the anterior surface of the basitrabecular process of the basisphenoid bone and passes forward, its fibres diverging somewhat, to be inserted into the anterior end of the pterygoid bone.

Innervation.—A twig from the mandibular ramus of the Vth nerve.

The Pterygo-quadratus is very similar to the same muscle in the Lacertilians. It arises from the posterior surface of the basitrabecular process of the basisphenoid and, passing caudad and laterad, is inserted into the posterior end of the pterygoid and lower end of the quadrate bone.

The Spheno-pterygoideus muscle is similar to, but more extensive than, the muscle in other reptiles. It arises from the palatine above the basitrabecular process of the basisphenoid and, its fibres radiating back and forth, is inserted into the middle third of the pterygoid bone.

Innervation.—These three muscles are all innervated by twigs from a common branch of the ramus mandibularis of the Vth nerve.

Hoffmann, following D'Alton, described a "Vomero-sphenoideus" muscle in *Python bivittatus.* In both the snakes I have studied I find a small muscle, which I would regard as a slip of the anterior spheno-pterygoideus muscle, which fits his description.

MUSCLES OF THE HYOID SEGMENT.

The Superficial ventral constrictor, Csv.2, is that muscle which Hoffmann described as the M. atlanto-epistropheo-hyoideus, but in the snakes which I have dissected it is much more extensive than in the *Python* as described by D'Alton, and on which Hoffmann's description is based. It is more than probable that the use of magnifying spectacles has enabled me to recognize more of the muscle than could be recognized without them.

The sheet of fibres is extremely tenuous, the origin is from the ligamentum nuchae and posterior end of the skull by means of the subdermal aponeurosis and the perimysia of the muscles of mastication. In *Pseudechis* the origin is almost confined to the aponeurotic structures over the depressor mandibulae, and the fibres pass from the origin, beginning with the more anterior of them, ventrad, then ventrad and caudad, and finally, almost directly caudad blending with the superficial longitudinal muscular sheath of the body. In *Python,* the Csv.2 is more distinct ; it arises from the ligamentum nuchae for a short distance behind the skull, and there is no actual origin from the aponeurotic structures over the depressor mandibulae. From their origin the fibres pass ventrad and swing rostrad towards the mid-line, but fade out before reaching it.

Innervation.—The anterior fibres of the muscle in both snakes are very definitely innervated by fine twigs from the motor division of the VIIth nerve which reaches the Csv.2 between the partes noto- and cephalo-gnathica of the depressor mandibulae.

The presence of a Constrictor Colli Spinalis in the *Python* is very doubtful. It has not been possible to demonstrate any spinal nerve supply to the muscle ; on the other hand, in the more extensive muscle of the colubrine snake, innervation by the first and second spinal nerves separately was demonstrated in every specimen dissected. There is, however, no indication of any boundary between the Sphincter colli facialis and the spinal sphincter. Experimental work is needed to determine boundaries.

The Depressor Mandibulae muscle recalls that of the Lacertilians, and more especially that of the Monitor lizard.

Pars Cephalognathica.—This is a remarkably massive and a compact muscle which arises from the back of the skull close to the mid-line, and from the posterior surface of the quadrate. The muscle is always separable into anterior, more superficial, and posterior, deeper, portions, and of these the latter is the larger. The plane of separation extends down almost to the mandible. The insertion of both portions is into the post-articular part of the surangular.

Innervation.—This is by several small twigs from the motor division of the VIIth nerve, which enter the muscle on the surface exposed on separation into its two parts.

Pars Notognathica.—This has an extensive origin by means of the aponeurosis, from the ligamentum nuchae for some distance behind the skull. The fasciculi converge as they pass rostrad, and ventrad, to be inserted by a very strong tendon into the surface of the anterior end of the quadrato-mandibular ligament.

Innervation.—This is by a single large branch of the motor division of the VIIth nerve which reaches its deep surface from behind the posterior margin of the pars cephalognathica.

The Hypobranchial Spinal Muscles.

The absence of the sternum alone would render the identification of these muscles a matter of some difficulty, but in addition to the loss of that structure their identification is made more difficult by the reduction in the hyoid apparatus and the transportation of the larynx very far forward and the development of the long protrusible tongue and its sheath.

The Hyoid apparatus is reduced to a narrow bow with a short anterior spur. This last lies just forward of the transverse level of the two jaw joints ; the thin arms of the bow extend back along the neck for some distance. This single hyoid arch is probably the second ; it appears too far back to be the ceratohyal.

The superficial sterno-hyoid and hyomandibular muscle is a forward continuation of the rectus abdominis. As it passes over the hyoid cornu its deeper fibres are bound thereto ; its anterior insertion is into the skin superficial to the parotid gland and to the lower edge of the mandible almost along its full length.

The lateral, Cervico-hyomandibular, muscle has an aponeurotic origin from the ligamentum nuchae behind the origin of the pars notognathica of the M. depressor mandibulae. Its fibres sweep forward ventrad and mediad, and have an aponeurotic insertion into the skin and posterior end of the mandible. The union of this aponeurosis of insertion with that of the pars notognathica gives the muscle an attachment to the lower edge of the quadrato-mandibularis ligament.

The muscle which is, in all probability, the homologue of the sterno-mastoid arises, in the snakes, from the deep surface of this last muscle about the middle of its length and passes rostrad and slightly dorsad. Tapering rapidly, the muscle is inserted, by a fine strong tendon, into the upper end of the quadrate between the two portions of the pars cephalognathica of the M. depressor mandibulae. Hoffmann designated this muscle the retractor ossis quadrati.

The Genioglossus appears to be represented by a small muscle which has not heretofore been observed, but which is present in both the snakes studied. The muscle arises from the inner surface of the mandible superficially to the Csv.1a. Its fibres pass more directly mediad and dorsad between the two halves of the submentalis to be inserted in part into the sheath of the tongue and in part into the side of the trachea just posterior to the larynx. In *Pseudechis* the latter fibres are quite separate from the former throughout their length and, moreover, in this form those inserted into the sheath of the tongue are distinctly gathered into a posterior and an anterior group.

The Geniohyoideus (pr.la.) is that muscle which Lubosch designated " geniotrachealis ", and Goppert " protractor laryngis ". It arises from the fore end of the dentary behind the origin of the M. genioglossus and, passing back and dorsally, is inserted into the side of the trachea a short distance behind the larynx.

The Hyo-glossus muscle (" Genio-hyoideus " of Lubosch) is apparently that which Goppert designated the retractor laryngis. The muscle is a narrow thin band of fibres which arise from the deep surface of the curve of the hyoid apparatus and, passing forward along the side of the trachea, are inserted thereinto just behind the insertion of the protractor.

A muscle which arises from and surrounds the free end of the hyoid cornu and passes forward to be inserted into the base of the sheath of the tongue was termed the hyo-glossus by Hoffmann. It appears more probable that it is the homologue of the thyro-hyoideus of the Lacertilians.

NATIONAL MUSEUM OF VICTORIA

6. Review.

The Ventral Superficial Constrictors.—Of these there are, constantly present in all the Lacertilian genera examined, three portions of the mandibular sheet and a continuous hyoid sheet. In addition there is, in some forms, the muscle which has been designated M. interhyoideus.

The obvious division, in a number of forms, of the Csv.1 into three parts raises the question of the homology of these to the divisions of the muscle observed in the Anamniota.

Past writers have failed altogether to recognize that the muscle does present itself in more or less well defined portions, excepting only Lightoller. He expresses the opinion that only two parts of the muscle call for recognition, a pars intermandibularis and a pars extramandibularis, and these he homologizes with the similarly-named portions of the Csv.1 in the Selachians.

Unfortunately, Lightoller did not study the bony fishes at all, believing them to be specialized, and on that account not throwing any light upon the serial homologies of the muscles throughout the vertebrata.

Lightoller, however, has drawn attention to the fact that the pars intermandibularis of the Csv.1 already, in certain of the Selachii, shows a division into anterior and posterior portions. Throughout the bony fishes, it will be remembered, this division of the anterior part of the Csv.1 into submentalis and intermandibularis muscles is of constant occurrence. Again, in the great majority of the Amphibia, the Csv.1 is divided very completely into these two components. In the Amphibia it was further observed that no pars extramandibularis is ever developed, and in this respect the Amphibia resemble the bony fishes. It was also observed that the submentalis of the amphibian muscle is placed on a slightly deeper plane than the rest of the muscle.

Now, taking all these facts into consideration, it would appear that the M. submentalis of the Lacertilian is probably the homologue of the submentalis of the Crocodilia, Emydura, and of the Amphibia. Like the last, it is placed in front of the rest of the muscle and occupies a deeper plane.

The partes intermandibularis and extramandibularis I have regarded as being, together, the homologue of the pars intermandibularis of the Amphibia.

To this conclusion I am led by the following considerations. There is no pars extramandibularis developed in any bony fish, any of the Dipnoi, or any other Amphibian. Further than this, the whole of the Csv.1 of the Lacertilians is developed medially to the rami of the lower jaw, and in early stages of the development it is attached on either side to the median surface of Meckel's cartilage. In these early stages there is no extension laterally to these cartilages, no pars extramandibularis. The extension laterally and dorsally to the ramus of the jaw appears to be conditioned entirely by the growth of the M. pterygoideus internus around the ventral edge and up over the lateral surface of the jaw. It is noteworthy that it is only after this muscle has so extended, and only as it does so, that the Csv.1 comes to have the extramandibular extension. There is, so far as my material permits me to judge, no example of any portion of the Csv.1 in any Lacertilian having an extramandibular attachment anteriorly to the anterior margin of the M. pterygoideus internus, nor in any reptile which has no portion of the M. pterygoideus internus arising on to the outer surface of the mandible, e.g. Chelonians and Crocodilia, and *Chameleon*.

It will be remembered that the Csv.1 of the Selachians was not divided, in any of the genera examined, into anterior and posterior divisions, except to the extent that the origin of the posterior portion was extramandibular, whilst that of the anterior portion was intermandibular. Even in this respect it was not possible to recognize any definite line of demarcation between the two parts. The origin, in nearly every case, extended gradually across the outer surface of the mandible. Actually, it will be remembered, the division was quite clearly stated to be one of anatomical convenience and not of actual separation, or definition.

In view of all the facts it appears probable that the posterior portion of the Csv.1, behind that which contributes to the submentalis of the Bony Fishes, the Amphibia and the Reptilia, is homologous throughout.

PART III. THE SAURIA. (*Continued.*)

THE AVES.

The Muscles of the Birds.
The Larynx and its Muscles.
Summary and Review of Sauropsidan Muscles.
Review of the Saurian Muscles.

THE MUSCLES OF THE BIRDS.

Eighteen birds have been dissected for this section of the work, but, as there is a marked similarity in the arrangement of the muscles, only those which present interesting features will be described in detail.

The conditions in *Gallus*, which is described fully, may be regarded as the normal, or typical, arrangement for the birds. The majority of those examined resemble it closely.

Gallus.

(Figs. 157–166.)

THE MUSCLES OF THE MANDIBULAR SEGMENT.

The ventral constrictor, Csv.1, presents no division into parts. It consists of a sheet of transverse fibres which arise on each side from the inner surface of the mandible for the greater part of its length and which are inserted into a median raphe.

Innervation.—This is, of course, by the mandibular ramus of the Vth nerve. The course of this nerve is almost exactly as in the Reptilia. The main trunk passes deeply between the pterygoid and temporo-masseteric groups of masticatory muscles, the terminal, mandibular, branch enters the canal in the mandible. The first branch of this to perforate the jaw-bone breaks up into three to five twigs as soon as it emerges; one of these supplies the whole of the motor fibres to the Csv.1.

Lubosch (1933, fig. 14) depicts the posterior margin of this muscle as trending caudad. I have dissected, in all, about forty specimens, and in every one of them I find the posterior margin to be almost exactly transverse, but I also find that the posterior limit of the origin is placed further back than he depicts it, whilst the posterior limit of the insertion is a little further forward.

The muscles of mastication are essentially similar to those of the reptiles. I have not, however, found any trace of the retractor anguli oris in any one of the many birds examined.

The Masseter muscle is a relatively thicker muscle in the fowl than it is in any reptile examined. It arises from a very strong fascia which is bound to the outer surface of the post-orbital process of the skull and to the anterior wall of the fibrous external auditory meatus.

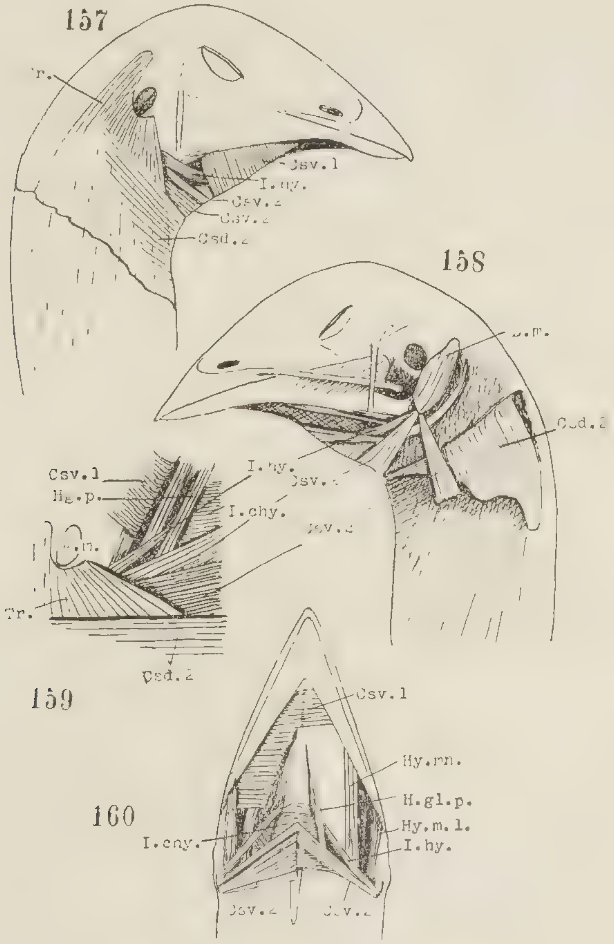
This fascia is, as it were, continued forward and ventrally along the superior margin of the muscle for about two-thirds of the length of that margin. The fasciculi arise from the outer surface of the post-orbital process and from the continuation of the fascia along the whole of its length. Their direction is ventrad and rostrad and they are inserted directly into the outer surface of the mandible well in front of the jaw joint.

The Temporalis muscle arises from the inferior margin and surface of the post-orbital process and from the skull in the temporal fossa deep to the M. massetericus. This temporal muscle is roughly pyramidal in shape. The apex of the pyramid is a short tendon which is inserted into the upper edge of the mandible, actually to the little tubercle upon that edge immediately above Meckel's fossa and which may be regarded as a much reduced coronoid process. The pyramid is, then, upside down, and the base is the origin of the muscle as described.

As the final portion of this work goes to the press I feel that some explanation of the absence of references to recent work is called for. The work was commenced in 1933 and progressed steadily till its completion in 1939. Delay in publication resulted from lack of available funds and the general uncertainty of conditions associated with the declaration of war. In 1942 the Trustees of the Australian Museum agreed to publish sections of the work from time to time as funds became available, and in 1944 a grant from the Commonwealth Scientific Publications Committee helped to expedite the completion of publication. I should like to express my gratitude to both those bodies, as well as to the Director of the Museum, Dr. A. B. Walkom, and to the Librarian, Mr. W. A. Rainbow, for invaluable assistance in the editing and printing of the memoir.

As a result of the delay, the work, in its reference to current research in comparative anatomy and embryology, is to a certain extent out of date. This has been unavoidable because my time has been wholly taken up in the discharge of my duties as Director of Medical Services of the Allied Works Council of the Commonwealth of Australia, and consequently I have had no opportunity of bringing the work up to date.—H.L.K.

The Quadrato-mandibularis muscle arises from the anterior process of the quadrate, and its fasciculi pass almost directly ventrad to be inserted on to the outer surface and lower edge of the mandible between the insertion of the M. massetericus and the joint. This muscle is a flat ribbon of tissue of no great thickness.



Figs. 157–160.—*Gallus.* Superficial muscles.

The pterygoideus externus muscle is a rounded bundle of fasciculi which arise from the wall of the skull below and just in front of the root of the post-orbital process. The muscle is clothed upon its anterior surface by a strong band of fascial fibres, and it is into this that the greater part of the fasciculi are inserted. The fascia gives the muscle a short tendinous insertion into the upper edge of the mandible medial to the insertion of the temporalis muscle.

The pterygoideus medius muscle appears as though it were an anterior extension of the M. quadrato-mandibularis. It arises from the upper edge and lateral surface of the anterior process of the quadrate bone. Its fibres pass ventrad, laterad, and rostrad, and are inserted along the upper edge of the mandible and along an upper strip of the internal surface thereof. The insertion of these fasciculi commences behind at the anterior edge of the M. quadrato-mandibularis and terminates at the same point as the most anterior point of insertion of the M. massetericus.

At its origin this muscle appears to be quite continuous with the anterior fasciculi of the M. quadrato-mandibularis, and, indeed it cannot be dissected free from that muscle. There is, however, a strong tendinous band running from the posterior point of origin of the muscle almost to the posterior edge of its insertion. This marks the limits of the two muscles, which are further indicated by the fact that the most anterior, like all the rest of the fasciculi of the M. quadrato-mandibularis, are inserted into the inferior edge of the external surface of the mandible, whilst the most posterior fasciculi of the M. pterygoideus medius stop short to be inserted into the superior edge.

The Pterygoideus internus is a very massive muscle and is best described in two portions. These two parts are intimately fused along their contiguous margins.

The Pars medialis arises from the posterior half of the inferior and median surfaces of the palatine bone and from the inferior and posterior surfaces of the pterygoid bone. The origin is in part directly from the palatine and pterygoid bones, and in part from a fascia which is attached to the inferior surface of the palatine bone and spreads out upon the inferior surface of the muscle. In the result the muscle receives an appearance of being spindle shaped and arising from the fascia. The muscle is inserted into the inner half of the inferior surface and posterior edge of the median half of the transverse process of the mandible, and also on to the whole of the superior surface of that process medial to the articular cavity. This last insertion is of the whole of the fibres which take their origin from the pterygoid bone, and there is a partial cleavage between this portion of the muscle and the rest of it, which suggests the imperfect separation of a M. pterygoideus posterior.

The Pars lateralis arises from the anterior half of the inferior and lateral surfaces of the palatine bone in a manner similar to the origin of the last muscle. In similar way it receives an appearance of being spindle shaped, as viewed from the inferior surface. Inferiorly these two muscles are intimately fused along their contiguous edges. Superiorly a cleavage exists between the muscles right to the ventral fascial membrane anteriorly and gradually becomes shallower as it is traced backwards. The insertion of the M. pterygoideus internus is into the inferior surface and posterior edge of the lateral half of the transverse process and the post-articular piece of the mandible.

The Spheno-pterygoideus muscle arises from the side wall of the skull medially to and only just above the pterygoid bone. It is inserted into superior and anterior surfaces of the pterygoid bone and into the upper edge and posterior surface of the anterior process of the quadrate bone.

THE MUSCLES OF THE HYOID SEGMENT.

In the course of his work upon the muscles of saurians, Lubosch (1933) describes and illustrates those of a few birds. His description of the superficial constrictor sheet in *Struthio* and in *Gallus* is accurate in respect of the morphology of the muscles. I find, however, that there is an error in his determination of the extent of the constrictor sheet innervated by the facial nerve.

The muscle which he regards as the hyoid portion of this sheet and indicates with the letters C.mv.hy. is innervated by the ninth nerve and the aboral portion of the sheet is not nearly so extensive as his illustrations depict. This last statement is based upon dissections and experimental investigation in the case of *Gallus*, but upon the dissections only for the birds generally.

The disposition of the various branches of nerves VII, IX and X were carefully determined in *Gallus* and their functions were then determined by stimulation.

Many experiments were carried out before all doubts as to the functions of the various branches were set at rest. In the early experiments the birds were pithed prior to the work, but later it was found that one had from twenty to thirty minutes in which to carry out the experiments after they were simply decapitated, before the muscles failed to respond to stimulation. In this work I had the able assistance of my son, Geoffrey L. Kesteven, and take pleasure in recording my indebtedness to him, and also to Professor H. Priestley for the loan of the electrical equipment for the work.

The facial nerve issues from its foramen behind the external auditory meatus medially to the fibrous posterior wall thereof. It at once gives off two twigs to the depressor mandibulae muscle. After a very short course against the posterior surface of that muscle the nerve crosses to the fascial plane in front of the hyoid cornu and divides into two branches. Both of these reach the deep surface of the dorsal facialis constrictor (Csd.2) in front of the anterior margin of the M. trapezius. The posterior, or more dorsal, branch is distributed entirely to the Csd.2. The more medial, and larger, branch gives off a branch anteriorly. This supplies the two portions of the Csv.2 and the M. interhyoideus. The rest of the nerve supplies only the ventral portion of the Csd.2.

The ninth and tenth nerves (Fig. 161) emerge close together deep to the emerging seventh. They are joined by a fairly thick commissure immediately outside their foramina of exit from the skull. Just a little way distal to this another commissure is present. This leaves the tenth and runs forward to join the ninth ; it also is quite short. Almost immediately beyond the point of junction of this last with the glosso-pharyngeal, the nerve which supplies the whole of the muscles of the floor of the mouth leaves this last. Experimental work showed this to be composed, as far as its motor fibres were concerned, of ninth nerve fibres only. If one severed the ninth nerve behind the second commissure, and then severed the first, one obtained no contractions of any of these muscles on stimulation of the proximal end of the vagus. Amongst the muscles which contracted was the "C.mv.hy." of Lubosch, present in *Gallus*, and precisely similar to that muscle in *Struthio* and *Dromaeus*.

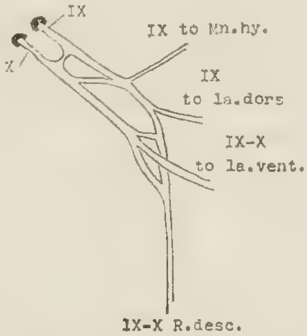


Fig. 161.—*Gallus*. Diagram of the main branches and anastomoses of the IXth and Xth nerves.
IX-X to la.dors., the nerve to the larynx ; IX-X to la.vent., the nerve to the deeper hypobranchial muscles ; IX to Mn.hy., the nerve to the superficial hypobranchial muscles ; IX-X R.desc., the descending gastro-intestinal trunk.

Beyond the nerve to the hypobranchial hyoid muscles, the ninth divides into its two terminal branches. One of these carries motor fibres to dorsal pharyngeal muscles, the other is the descending branch of the nerve.

Beyond the second commissure, and at an appreciable distance from it, the vagus divides into three. Two of these join the descending branch of the ninth. The third carries motor fibres to ventral pharyngeal muscles and the recurrent laryngeal fibres.

These same nerves were dissected out in *Struthio*, *Dromaeus*, *Anas*, *Phalacrocorax* and *Calyptorhynchus* ; they were also studied in serial sections of a number of late embryos, and in no case was any difference worthy of record noted. It is, therefore, assumed that the innervation of similar muscles is the same throughout the birds.

Stimulation of the two branches of the seventh nerve to the Csd.2 produced contractions only over the small region occupied by the muscle depicted in my figure 157. Actually, the extent of the muscle so depicted was determined by dissection before the experimental work was carried out, as also was the innervation of the "C.mv.hy." by the ninth nerve, and it was these discrepancies which caused me to undertake the experimental work.

The greater portion of the "C2.dv.abor." of Lubosch is portion of the general platysma myoides and may be designated constrictor colli spinalis, since it is probably completely homologous with the similarly named muscle in the Chelonians and some other reptiles.

The innervation of the deeper muscles presumably innervated by the ninth nerve, as indicated by dissections, was not definitely determined by the experimental method. That complete and clean exposure of the muscles necessary for quite satisfactory observations could not be completed before the muscles failed to respond to nerve stimulation.

The three parts of the Superficial constrictor are placed upon successively deeper planes, from behind forward.

The posterior portion of the superficial facialis constrictor (Csd.2) lies immediately beneath the skin. Its anterior border is found immediately behind the posterior margin of the depressor mandibulae muscle. It arises from the fascia dorsalis about one-third of the distance down from the mid-dorsal line to the mid-lateral line of the neck. This is the level of origin of the more anterior fibres; as one proceeds caudad one finds that the origin is placed gradually lower and lower. In other words, the fibres lose in length at the expense of their upper ends. They are all inserted into a medial ventral raphe. Their direction is almost precisely at right angles to the long axis of the neck, with a very slight inclination caudad. The fibres of this muscle lie upon the extensive trapezius muscle (Tr.), and the anterior fibres are nearly parallel with the most median fibres of that muscle as they tend to a transverse direction on either side of the mid-line.

The Csv.2 is present in two parts, the more superficial portion of the muscle (Csv.2) arises from a short line upon the outer surface of the post-articular piece of the mandible. From this origin the fasciculi pass ventrad and mediad to be inserted into the mid-ventral raphe. The muscle is broader at its insertion than at its origin, and the anterior fibres have an inclination rostrad. The muscle is placed upon a deeper plane than the Csd.2. At its origin it lies deep to the trapezius muscle, which, in turn, lies deep to the Csd.2. At its insertion, careful dissection reveals that there is a definite fine fascia overlying it which continues forward the plane of the Csd.2, although the median raphe of the one becomes intimately blended with that of the other.

The deeper and more anterior portion of the muscle arises from a similar short line in front of the last muscle and its fibres pass mediad and ventrad to be inserted into a mid-ventral raphe. The more posterior fibres of this muscle lie dorsally to the anterior fibres of the last and their respective median raphes do not combine. On the other hand, the insertion of the anterior portion is very intimately bound to the ventral surface of the body of the hyoid.

The Depressor Mandibulae muscle is a solid oblong mass of fibres which arise from the posterior, fibrous, wall of the external auditory cavity and from the surface of the skull dorsally thereto. The muscle lies deep to the anterior end of the M. trapezius. Its direction is, from its origin, ventrad and laterad, with a slight curve rostrad in its posterior fibres. It is inserted into the upper part of the external surface and practically the whole of the internal surface of the post-articular piece of the mandible.

It should be noted that this depressor mandibulae can represent only the pars cephalognathica of the muscle in the reptiles; there is no trace of any division into two heads. It will save repetition to state that no representative of the pars notognathica has been found in any bird investigated.

The Interhyoideus muscle arises in front of the Csv.2, and deep to the deeper portion, from the articular bone; it is a thick cord-like muscle which runs forward and mediad. It crosses the M. hyo-mandibularis superficially and then passes deep to the M. hyo-glossus posterior to reach the dorsal surface of the rod-like anterior portion of the hyoid body. The two muscles of opposite sides meet in a common line of insertion along the centre of this surface.

Muscles Innervated by the Ninth Nerve.

(Figs. 160–167.)

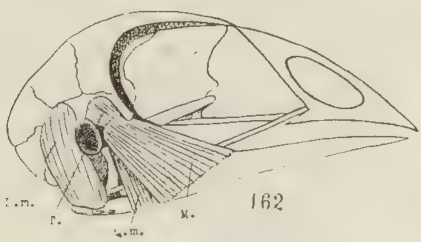
The M. hyomandibularis arises from the posterior half of the length of the hyoid cornu, clothing it completely with its fasciculi. The muscle divides into medial and lateral portions which are inserted, one behind the other, into the inner surface of the mandible. The smaller, lateral, portion is inserted superficially to the Csv.1, the medial portion deep to it.

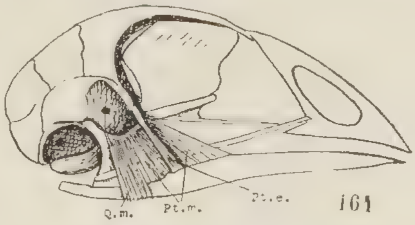
The M. hyoglossus posterior arises from the anterior half of the length of the hyoid cornu. Although this is a thin, cord-like muscle, its origin clothes all those surfaces of the cornu in this part of its length not covered by the M. intercerato-hyoideus. The fasciculi are inserted into a very fine tendon which loses itself in the tough tissues of the anterior end of the tongue.

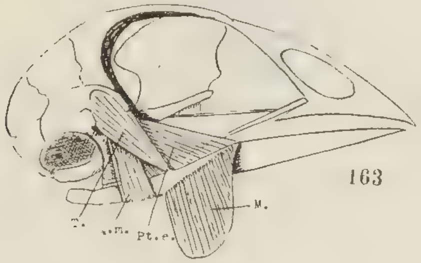
The M. Thyro-hyoideus is a massive muscle which arises from the ventral surface of the thyroid cartilage, from a small area of the thyreo-tracheal membrane and from the wall of the pharynx close to these two structures. Its fibres pass directly forward, converging slightly to be inserted into the dorsal surface of the body of the hyoid behind the insertion of the M. interhyoideus.

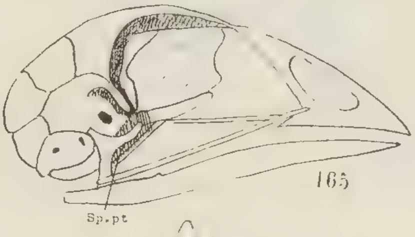
The Interceratohyoideus muscle is a remarkably thick sheet of fibres which arise from one hyoid cornu, cross the urostyle, and are inserted into the other cornu. The muscle commences, in front, just behind the body of the hyoid and its posterior margin is about two-thirds of the length of the urostyle further back.

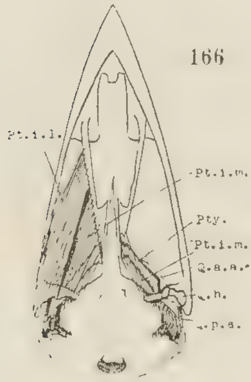
The Hyoglossus anterior muscle arises from the anterior end of the body of the hyoid and is inserted into the fibrous tissue of the tongue. The most ventral fibres of this muscle are differentiated from the rest; they run directly forward along the ventrum of the tongue between the tendons of the posterior hyoglossus muscle. The other fibres have a direction forward, dorsad and slightly laterad, outside the tendons.

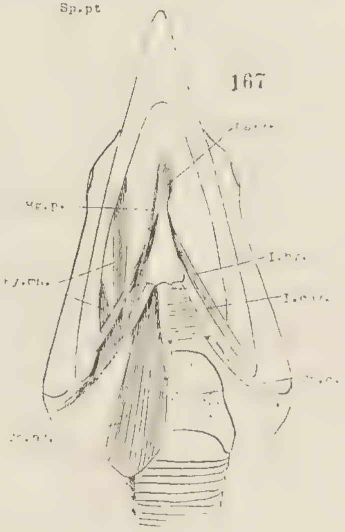












Figs. 162–166.—*Gallus*. The muscles of mastication.
Fig. 167.—*Gallus*. The hypobranchial muscles.

Dromaeus and *Struthio*.

(Figs. 168–171.)

These two birds resemble one another so closely that they may be described together.

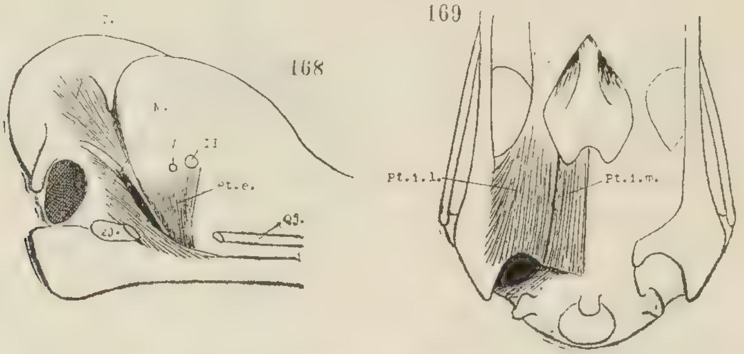
THE MUSCLES OF THE MANDIBULAR SEGMENT.

The Csv.1a is not to be found.

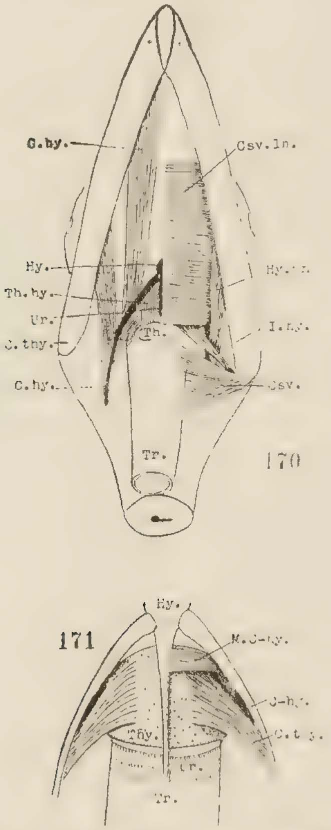
The Csv.1b is a very typical muscle. All the fibres pass directly transversely and are inserted into a median raphe. The line of origin is placed fairly high on the inner surface of the mandible, about one-third of its depth from the dorsal edge. This line commences behind just in front of the insertion of the muscles of mastication and extends forward to near the junction of the middle and anterior thirds of the length of the mandible.

The Masseter muscle arises from the lower part of the temporal fossa and from the inferior post-orbital process above the quadrate. The fibres run forward and ventrally and are inserted on to the upper edge of the mandible and a narrow area on the outer surface close to the dorsal edge and into a more extensive area on the inner surface.

The Temporalis muscle arises from the upper part of the temporal fossa, from the inner surface of the superior post-orbital process, and from a small area of the surface of the alisphenoid bone in the posterior wall of the orbit. The fibres are all inserted into a strong rounded tendon which is inserted into the inner surface of the mandible below the foramen for the mandibular branch of the fifth nerve.



Figs. 168, 169.—*Struthio.* The muscles of mastication.



Figs. 170, 171.—*Dromaeus.* The ventral muscles.

The Quadrato-mandibularis muscle is apparently completely fused with the deep surface of the M. massetericus; that portion of the muscle which arises from the inferior post-orbital process actually arises almost in the situation of the origin of the quadrato-mandibularis muscle in other birds. It will be remembered that the otic process of the quadrate, which stands out freely in the great majority of birds, is very nearly covered by the inferior post-orbital process in the Emu and the Ostrich and their allies.

The Pterygoideus externus muscle arises from the area of origin, is quite narrow, and commences in front of the optic foramen and extends back to the junction of the presphenoid to the basisphenoid bone. It is a flat sheet of fibres which pass, almost horizontally, laterad, converging to be inserted into a narrow area along the inner surface of the mandible below the insertion of the M. massetericus.

The Pterygoideus medius muscle is quite continuous with the deep surface of the M. pterygoideus externus; it arises from the lateral surface of the palatine process of the quadrate. Its fasciculi run horizontally laterad, with a caudad inclination, to be inserted below the M. pterygoideus externus.

The Pterygoideus internus muscle is exceedingly massive. As is usual in the birds, medial and lateral parts may be recognized, although they are but poorly delimited. The pars lateralis arises from the lateral margin and inferior surface of the posterior plate of the palatine bone. The fibres run caudad and are inserted on the ventral edge of the ramus of the mandible and on the ventral surface of the expanded articular bone. The pars medialis arises from the inner margin of the expanded plate of the palatine and of the posterior plate of the vomer and from the ventral surface of the pterygoid bone immediately behind it. The insertion of the lateral fibres of this portion of the muscle is on to that portion of the ventral, expanded surface of the articular bone not occupied by the insertion of the pars lateralis. The remainder of this muscle probably represents the M. spheno-pterygoideus, which is, otherwise, not represented. The portion in question constitutes about the medial half of the muscle. All these fibres are inserted into a strong fascial band which binds the articular to the basisphenoid, behind the basipterygoid process, and also extends across the basisphenoid bone almost to the midline, just in front of the eustachian canal, where that leaves the tympanic cavity, and the anterior opening of the canal which carries the ramus palatinus facialis and the palatine artery. It will be noted that, if this be the spheno-pterygoideus muscle, its origin and insertion have both been shifted; its situation alone justifies the suggestion. In view of the fact that the palate is rigid, it appears possible that this muscle functions in some way to assist deglutition.

The Levator quadrati muscle is composed of short fibres which arise from the basisphenoid bone in front of and above the basipterygoid process and pass to the concave, medial surface of the pterygoid process of the quadrate bone.

THE MUSCLES OF THE HYOID SEGMENT.

The Csd.2 was not found, but this was possibly because the muscle is very fine, poorly developed, and was not distinguishable on the roughened surface caused by the deep insertion of the feathers and by their erector and depressor muscles, specialized slips of the general platysma myoides.

The Csv.2 is the only representative found of the constrictor colli facialis. Its fibres arise, close together, from the fascia dorsalis just behind the angle of the jaw. The fasciculi diverge backwards and forwards as they pass ventrad and mediad. The muscle is imperfectly divided into anterior and posterior parts. The pars posterior is made up of those fibres which diverge caudad and those with a direct transverse direction. The pars anterior, with forward trending fasciculi, extends across the ventral surface of the trachea, its most anterior fibres meeting their antimeres in the midline.

The Interhyoideus muscle arises beneath the Csv.2. Its fasciculi are gathered to form a rounded, almost cord-like, muscle which runs forward and medially to flatten out somewhat and be inserted into the urostyle immediately behind the body of the hyoid and under cover of the posterior fasciculi of the Csv.1b.

The Depressor mandibulae muscle is a perfectly typical avian muscle which arises from the skull behind and above the external auditory meatus and from the posterior fibrous wall of that cavity, and is inserted into the articular bone. There is no trace of any division into two parts.

The facial nerve is essentially similar in all respects to that of *Gallus*, but the course of the ramus palatinus is of interest. I have previously recorded the fact that this nerve, in *Dromaeus*, runs forward below the basipterygoid process (Kesteven, 1941*a*). It was then suggested that Brock (1937) had mistaken a small branch of the nerve which runs forward below the process for the ramus itself, in *Struthio*. I have now to record that the course of this nerve and its branches is absolutely the same in both forms.

Muscles Innervated by the Ninth Nerve.

The Hyomandibularis muscle arises from the posterior third of the length of the hyoid cornu and its fibres run straight forward to be inserted into the inner surface of the mandible superficially to the posterior half of the Csv.1b.

The Geniohyoideus muscle is a flat sheet of fibres which arises from the outer side of the anterior two-thirds of the length of the hyoid cornu. Its fasciculi run straight forward to be inserted into the inner surface of the mandible along a line which commences in front at the symphysis and runs back along about one-half of the length of the ramus of the lower jaw and is situated just deep to the line of insertion of the Csv.1b. The two median edges of this pair of muscles are appreciably thicker than the lateral edge. The muscle lies between the mucosa of the mouth and the upper surface of the Csv.1b.

The Thyro-hyoideus muscle is a relatively thick sheet of fibres which arise from the posterior margin of the ventral surface of the thyroid cartilage and are inserted into the hyoid cornu close to the body of the hyoid.

The Ceratohyoideus muscle is a short bundle of fibres which arise from the anterior end of the hyoid cornu and pass directly transversely to be inserted into the proximal end of the urostyle.

The Ceratothyroideus arises from the hyoid cornu opposite the upper end of the trachea and is inserted into the ventral surface of the thyroid cartilage. This is the C2.mv.hy. of Lubosch.

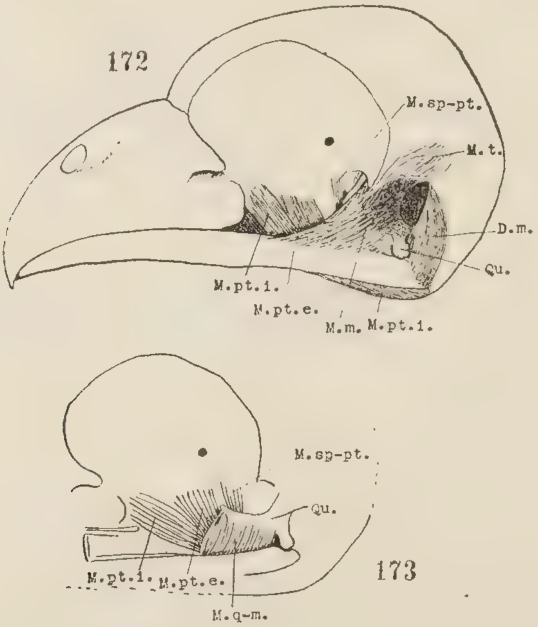
The last two muscles lie deep to the M. thyrohyoideus.

Podargus.

(Figs. 172–173.)

The Frog Mouth Owl is one of the birds in which the fronto-parietal joint functions to permit of the elevation of the upper beak. The movement is by no means as free as in the Parrots and Cockatoos, but is quite definite. This form was, therefore, dissected in order to compare its muscular mechanism with that of those other birds ; contrary to expectation, there was no trace of the peculiar modification of the arrangement of the pterygoid muscles which the parrots exhibit.

Before proceeding to the description of the muscles of mastication, it may be recorded that the other muscles present only minor differences from the typical avian arrangement.



Figs. 172, 173.—*Podargus.* The muscles of mastication.

THE MUSCLES OF MASTICATION.

In both the Owls and the Eagles the posterior wall of the orbit is made nearly complete by the extensive post-orbital process. This extends so far ventrad that it closes the temporal fossa from the orbit and, as a result, when the eye and its muscles have been taken from the orbit, little is seen of the muscles which, in the generality of birds, form its posterior wall. Although this is so, the muscles of mastication conform fairly closely to the typical avian arrangement.

The origin of the Temporal and Masseteric muscles is, as usual, from the temporal fossa. They and the M. quadratomandibularis are so intimately fused at their contactual surfaces that it is not possible to define them one from the other. Their origin is from the whole of the temporal fossa, the front wall of the external auditory meatus (here supplied by the extensive post-orbital process), the roof of the meatus, and the posterior and lateral surfaces of the quadrate and its articular ramus. Those fasciculi arising from the temporal fossa and the walls of the meatus may be regarded as constituting the M. temporalis. These fibres are inserted into a bifid tendon whose fan-like proximal ends lie buried in the muscle, and which is inserted, itself, into the inner side of the mandible above the foramen for nerve V3. The mass of fibres which arise from the outer surface of the more superficial of the bifurcations of the tendon and find their insertion into the dorsal edge and outer surface of a small area of the hinder end of the mandible, may be regarded as constituting the M. massetericus. All the fibres arising from the quadrate and its articular ramus are inserted into the posterior end of the mandible behind and below the insertion of the M. temporalis tendon. These fibres constitute the M. quadratomandibularis.

A short length of the temporalis tendon is visible below the post-orbital process between the masseteric fibres behind it and the anterior fibres of the M. quadratomandibularis in front.

The pterygoid muscles are also intimately fused at their contactual surfaces so that they may not be accurately defined.

The M. pterygoideus externus may be regarded as being constituted by fibres which arise from the whole of the lateral surface of the pterygoid bone. The fibres converge as they pass caudad and laterad to be inserted on to the inner edge of the expanded articular portion of the mandible.

The M. pterygoideus internus arises from both surfaces of the posterior end of the palatine bone and, by a small separate head, from the fascia joining the palatine bone to the mandible just behind the posterior point of contact of the two bones. The posterior half of the superior surface, the anterior half of the inferior surface, and the whole of the lateral edge of the muscle are clothed by a strong fascial sheath. The fasciculi of the anterior portion of the muscle are inserted into the dorsum of the ventral sheath, whilst the fasciculi of the posterior portion arise from the ventrum of the dorsal sheath and are inserted on to the inferior surface of the articular bone and edge of the mandible in front of it.

The M. sphenopterygoideus is intimately fused with the medial edge of the M. pterygoideus internus and the inferior surface of the M. pterygoideus externus. An examination of the inferior surface of the M. pterygoideus internus reveals a muscle which, at first sight, appears to be quite similar to the pars medialis of this muscle, as seen in the generality of birds. More careful examination discloses that the majority of the fasciculi of this muscle arise from the inferior surface and a narrow area along the inferior edge of the lateral surface of the pterygoid bone. These fasciculi pass forward to be inserted into the ventral fibrous sheath of the muscle. The sheath itself is attached in front to the inner margin of the palatine bone.

Apparently we have here a modification of the pterygoid muscles, whereby the pars medialis of the internal pterygoid and most of the fibres of the sphenopterygoid muscle have been converted into a depressor of the upper jaw.

A few perfectly typical fibres of the M. sphenopterygoideus pass laterad and caudad from the hinder end of the sphenoid bone to the pterygoid close to the pterygo-sphenoid articulation.

Eurystomus.

(Figs. 174–175.)

THE MUSCLES OF THE MANDIBULAR SEGMENT.

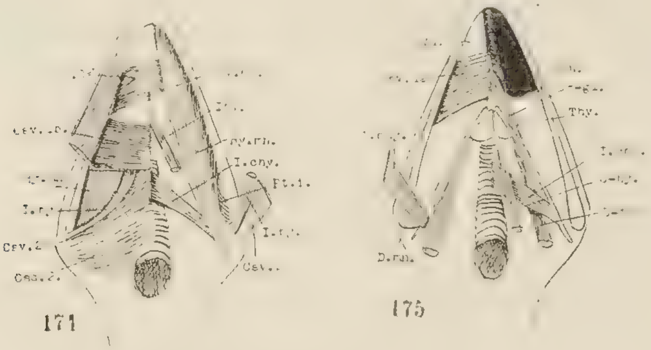
The Csv.1 is of particular interest because it is more definitely divided into the Mm. submentalis and intermandibularis than in any other bird dissected.

The M. submentalis (Csv.1a) is composed of a thin layer of fasciculi which extend uninterruptedly from one mandible to the other. These do not constitute a continuous muscle layer except at their posterior margin, but each fasciculus is separated by a space as wide as the fasciculus is broad. The fibres do not run straight across but are curved forward to the centre.

The M. intermandibularis (Csv.1b) is a much thicker sheet of fibres which run directly transversely. The posterior half of these are inserted into a median raphe, the rest are uninterrupted.

Both these muscles are inserted deep to the M. hyomandibularis.

The M. massetericus arises from the lower and posterior portion of the temporal fossa and from the upper end of the otic process of the quadrate. The greater part of the fibres arising from the temporal fossa are inserted into the upper edge and a narrow area close thereto on the outer side of the mandible. The deeper of these fibres and those arising from the upper part of the temporal region are inserted on to the tendon of the M. temporalis, which runs ventrad and rostrad along the anterior edge of the muscle. Those fibres which arise from the quadrate bone are inserted into the medial surface of the surangular, above and behind the foramen for nerve V. There is no cleavage plane between the last fibres and the posterior fibres of the M. pterygoideus medius.



Figs. 174, 175.—*Eurystomus.* Ventral muscles.
D.m., M. depressor mandibulae; H.gl., M. hyoglossus; Hy.mn., M. hyomandibularis; I.chy., M. interceratohyoideus; I.hy., M. interhyoideus; Mu., mucosa of the mouth seen from below; Pt.i., M. pterygoideus internus; S.hy., M. sternohyoideus; S.thy., M. sternothyroideus.

The M. temporalis arises from the upper portion of the temporal fossa and from the posterior surface of the post-orbital process. The fasciculi are all inserted into a strong tendon which is inserted into the mandible just above and in front of the foramen for the nerve V3.

The M. quadratomandibularis arises from the lateral surface of the pterygoid process of the quadrate, and its fasciculi run horizontally to be inserted into the medial surface of the mandible. The area of this insertion is almost equal in length to the area of origin, but is situated a little posteriorly to it.

The M. pterygoideus externus arises from the wall of the orbit dorsally and laterally to the prootic foramen. Its fasciculi are all inserted into a tendon which is inserted into the dorsal surface of the mandible just behind and medial to the foramen for nerve V3.

The M. pterygoideus medius may be most conveniently described in two portions. The pars posterior arises from the outer surfaces of the body, the processus oticus and the ramus articularis of the quadrate. The more ventral fibres are nearly horizontal, the more superficial nearly vertical as they pass to their insertion on to the mandible. This portion of the muscle is only partially separated from the deep surface of the M. massetericus by a narrow, very strong fascial band which extends from the tip of the otic process of the quadrate to the mandible, deep to the posterior end of the area of insertion of the M. massetericus. The pars anterior arises from the ventral edge of the pterygoid process of the quadrate in front of and deep to the M. pterygoideus externus. The fasciculi run ventrad, caudad and laterad to be inserted, with those of the pars posterior, into the dorso-medial surface of the mandible medially to the insertion of the M. massetericus and behind that of the M. pterygoideus externus.

The M. pterygoideus internus presents the usual avian feature of incomplete division into medial and lateral parts. The pars lateralis arises from both surfaces of the expanded posterior end of the palatine bone. On the dorsal surface this area extends forward to underlie the hinder end of the nasal capsule. On the ventral surface it stops short at the transverse level of the planum ant-orbitale above it. A plane of incomplete separation between dorsal and ventral portions of the muscle is formed by a delicate fascia which extends back for some distance in the plane of the edge of the palatine bone. The pars medialis arises from a medial strip of the area just described and from the dorsal, ventral and lateral surfaces of almost the full length of the pterygoid bone and from a small area on the side of the presphenoid just in front of the spheno-pterygoid articulation. The whole of the fasciculi are inserted into the anterior surface of the articular bone, without any trace of division.

The M. spheno-quadratus arises from the lateral surface of the sphenoid bone medially to the pterygoid process of the quadrate. It is into the medial and part of the dorsal surface of this process that all the fasciculi are inserted.

The Fifth Nerve and its Branches.

The foramen prooticum comes into view when the last-mentioned muscle is pulled forward and medially. The nerves to the temporalis and massetericus muscles pass dorsad and rostrad against the anterior surface of the M. temporalis, which lies in contact with the M. pterygoideus externus. A sensory branch of the fifth nerve also emerges from between these muscles but at a higher level. The twigs of this sensory branch are distributed to the temporal region of the head. The nerve to the M. pterygoideus internus runs forward medially to and below the tendon of its muscle, whilst the main ramus mandibularis runs ventrad and rostrad between its tendon and that of the M. temporalis. The nerves to the M. pterygoideus externus itself and to the M. pterygoideus medius are very short and reach their destination under cover of the former.

The maxillary ramus of the fifth nerve emerges between the tendons of this muscle and the M. temporalis and then turns rostrad superficially to the tendon of the former. In its further course across the floor of the orbit it lies upon the dorsal surface of the M. pterygoideus internus. As it crosses the M. pterygoideus externus it, of course, also passes externally to the more deeply placed M. pterygoideus medius.

The "myloid" branch of the fifth nerve emerges from the medial surface of the mandible about the middle of the width of the M. Csv.1b and superficially to that muscle. Three twigs are given to this muscle, and the main branch then continues forward just medially to the medial border of the M. hyomandibularis. The terminal branch gives four small twigs to the M. Csv.1a and then finally breaks up in front of that muscle. No twigs were observed to terminate on or in the M. hyomandibularis.

THE MUSCLES OF THE HYOID SEGMENT.

The Constrictor colli facialis dorsalis (Csd.2) is a thin sheet of diverging fibres, which arise from the fascia dorsalis behind the angle of the jaw, and slightly dorsal thereto, and spread out as they pass ventrad, curving rostrad, to reach the mid-ventral line below the anterior end of the trachea, where they are inserted into a median raphe.

The Constrictor colli facialis ventralis arises from the fascia of the M. depressor mandibulae and from the postero-ventral and medial corner of the os angulare. The fasciculi run mediad and curve rostrad to be inserted into a median raphe which lies below the M. interceratohyoideus which, in turn, lies beneath the extreme anterior end of the trachea. There is no indication of any division of this muscle into two parts as in *Gallus*.

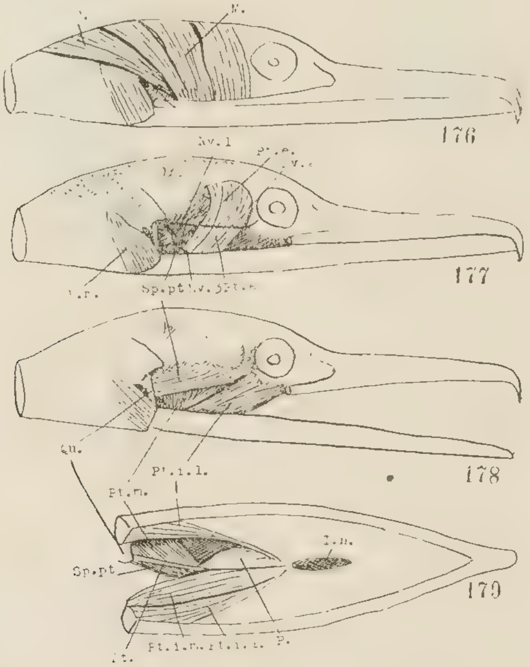
The M. interhyoideus arises just in front of the origin of the last muscle and partly under cover of its anterior edge. This muscle arises as a narrow thin ribbon compounded of much fibrous tissue, but rapidly increases in thickness and slightly in width, to form a relatively stout cord which runs forward and medially to be inserted into the lateral edge of the posterior end of the body of the hyoid and into the anterior end of the cornu just behind its articulation with the body.

The M. depressor mandibulae is a perfectly typical avian muscle.

The Facial nerve emerges behind the depth of the external auditory meatus, between the M. depressor mandibulae and the posterior end of the hyoid cornu, and divides into its several branches almost at once. The two nerves to the M. depressor mandibulae are very short and enter the postero-medial edge of the muscle. The nerve to the M. Csd.2 runs dorsad and caudad along the posterior edge of the M. depressor mandibulae, crosses the posterior end of the hyoid cornu, then, reaching the anterior margin of the M. Csd.2, it turns rostrad and ventrad beneath the muscle to break up into several fine twigs. The motor nerve to the M. Csv.2 and the M. interhyoideus crosses the muscle-covered hyoid cornu superficially and then runs forward and mediad along its medial border. The nerve finally breaks up into its terminal twigs on the deep surface of the two muscles.

The Muscles Innervated by the Ninth, Tenth and First Spinal Nerves.

The M. hyomandibularis is a more extensive muscle than is common amongst the birds and includes the genio-hyoideus completely fused with it. It arises, as usual, from an origin which completely clothes the posterior end of the hyoid cornu and extends forward along about one-third of its length. The fibres run forward and are inserted along a line on the inner surface of the mandible which extends from just in front of the area of insertion of the M. pterygoideus internus right forward to the symphysis. Posteriorly the muscle lies deep to the Mm. Csv.2 and interhyoideus; anteriorly it is superficial to the insertions and lateral portions of the Mm. Csv.1a and Csv.1b.



Figs. 176–179.—*Phalacrocorax.* Muscles of mastication. D.m., M. depressor mandibulae; I.n., internal naris; M., M. massetericus; Nv^1., the profundus branch of the Vth nerve; Nv^2., the maxillary branch of the Vth nerve; P., palatine bone; Pt., pterygoid bone; Pt.e., M. pterygoideus externus; Pt.i.l. & Pt.i.m., partes lateralis and medialis of the M. pterygoideus internus; Pt.m., M. pterygoideus medius; Qu., quadrate; Sp.pt., M. spheno-pterygoideus; T., M. temporalis.

The M. interceratohyoideus arises from a short line on the medial surface of the hyoid cornu well towards the posterior end thereof. Its fibres spread out to form a relatively thin sheet deep to the Csv.2. Their insertion is into a median raphe.

The M. hyoglossus arises from the outer, dorsal and ventral surfaces of the anterior one-third of the length of the hyoid cornu. The fasciculi are gathered into a rounded cord-like muscle which runs forward, mediad and dorsad to be inserted into the tough fibrous matrix of the tongue, reaching it, of course, from below.

There is no M. thyrohyoideus present in this bird.

The M. sternohyoideus is a long oval cord-like muscle which (it is believed) arises from the anterior margin of the sternum and runs forward beneath the Mm. constrictor colli spinalis, constrictores colli fascialis dorsalis and ventralis to be inserted by a fine tendon into the postero-medial margin of the body of the hyoid just medially to the articulation of the cornu.

The M. sternothyroideus is a similar but slightly thicker muscle which lies laterally to the last, and (probably) has a similar origin. This muscle is deep to the M. interceratohyoideus as well as to those mentioned as superficial to the last. Its insertion is into the postero-lateral corner of the thyroid cartilage.

Phalacrocorax.

(Figs. 176–179.)

The muscles of mastication of *Phalacrocorax* are of particular interest. They resemble those of the Lacertilia more closely than do those of any other avian type examined. So closely do they resemble the muscles of the Lizards that there is no room for doubt as to the serial homology of the muscles in the two groups, and *Phalacrocorax* and its allies serve as the interpreter of the masticatory muscles of the whole of the Aves.

In this bird, as in *Physignathus*, we recognize at once two main groups of these muscles: one, the temporo-masseteric, lying superficially to the second and third divisions of the Vth nerve, the other, the pterygoid, lying deep to those nerves.

Although three members of the temporo-masseteric group of muscles are quite certainly present, as indicated by differences in the direction of their fasciculi and of origin and insertion, they are so intimately fused that it is not possible to indicate with any degree of confidence what may be the real limits of these three muscles. The three which are present are the Masseter, the Temporalis and the Quadrato-mandibularis. Of the three the M. massetericus is the most bulky and most superficial. It arises from a large area of the skull wall behind the orbit and extending up to the mid-dorsal line. Its insertion is entirely fleshy. The M. temporalis arises further back, extending beyond the posterior limit of the skull to arise from the mid-dorsal septum. Its fibres run rostrad, ventrad and laterad and are, for the most part, gathered on to a tendon which burrows forward between the fasciculi of the other two muscles to be inserted on to the upper edge of the mandible. The Quadrato-mandibularis muscle arises from the quadrate and from the skull wall close to it, and its fibres run ventrad to the mandible, passing deep to the last muscle.

The M. pterygoideus medius arises, again in the same sense, quite typically from the pterygoid bone and its fibres pass nearly horizontally but with an inclination ventrad and caudad to be inserted into the inner surface of the mandible behind the insertion of the last muscle.

The M. pterygoideus internus, though essentially similar to the lacertilian muscle, introduces a feature not present in any reptile, but apparently characteristic of, and certainly very prevalent amongst, the birds. The muscle is incompletely divided into lateral and internal parts. The pars lateralis arises from the lateral edge and upper surface of the os palatinum. This origin is largely tendinous and the inferior surface of the muscle is clothed by a membranous expansion of the tendon. This membrane gives their point of origin to the greater part of the fibres. The insertion is into the inner surface and lower edge of the mandible far back near the joint. The pars medialis arises from the inferior surface of the expanded palatine plate of the os palatinum. The greater part of this origin is fleshy, but there is also a strong membranous origin from the antero-lateral edge of the plate. Here also this membrane clothes the ventral surface of the muscle and gives origin to many fibres. The insertion is into the inferior surface of the laterally expanded articular process of the mandible. (Note.—In the illustration of the ventral aspect of these muscles, the articular process of the mandible has been removed from the right-hand mandible, in order the better to display the other muscles.)

The M. spheno-pterygoideus arises from the wall of the skull, low down along a line immediately dorsal to the level of the pterygoid bone. The fibres pass nearly horizontally caudad and laterad to be inserted into the pterygoid bone and into the shaft of the os quadratum.

There are here two completely fused muscles, the M. spheno-pterygoideus and the M. levator quadrati. We are enabled to make this statement at this stage because dissections upon other avian types have shown that both muscles are usually present. We may also remark that a M. pterygoideus posterior is also quite well differentiated in some birds.

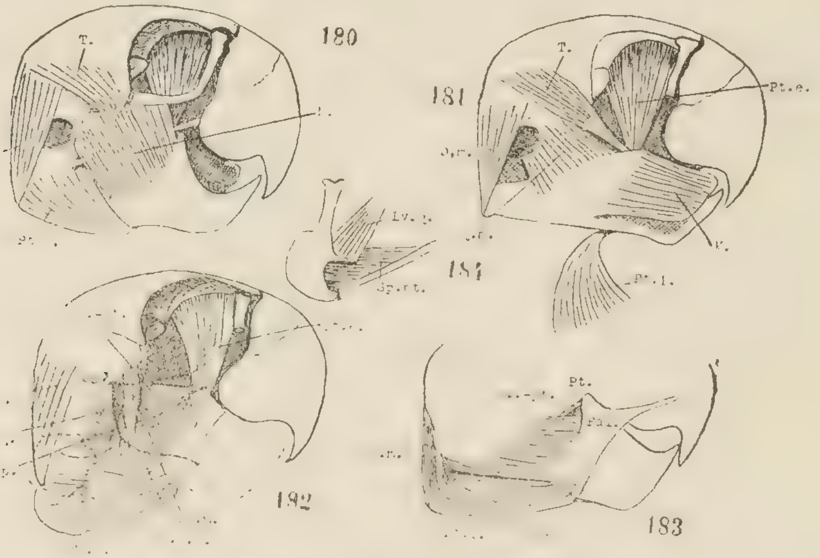
Calyptorhynchus, *Cacatua* and *Polytelis*.

(Figs. 180–184.)

The muscles of mastication of the parrots and cockatoos differ markedly from those of the fowl and the heron, and are peculiar.

The Masseter muscle is an extensive sheet of fibres which arise from the quadrato-jugal arch, from the fascia attached to the lower margin of the sub-ocular portion of the pre-orbital bone, and the post-orbital process, and from a fascia which is attached above to the inferior margin of the last process and below to the upper margin of a short pre-otic process. This extensive muscle encloses almost the whole length of the quadrato-jugal bar within its thickness. Its deeper fibres arise from the fascial sheets deep to the bar, whilst its superficial fibres arise from the fascia superficial to it.

The fibres are inserted directly upon the outer surface of the mandible along a line which begins close to the inferior margin and runs diagonally upward and forward to end close to the upper margin just behind the angle of the gape.



Figs. 180–182.—*Calyptorhynchus.* Muscles of mastication, lateral view.
D.M., M. depressor mandibulae; Lv.q., M. levator quadrati; M., M. massetericus; Pal., palatine bone; Pt., pterygoid bone; Pt.e., M. pterygoideus externus; Pt.i.l. & Pt.i.m., partes lateralis and medialis of the M. pterygoideus internus; Pt.m., M. pterygoideus medius; Pt.p., M. pterygoideus posterior; Sp.pt., M. sphenopterygoideus; T., M. temporalis.

Fig. 183.—*Calyptorhynchus.* Muscles of mastication, medial view.
For explanatory letters see Figures 180–182.

Fig. 184.—*Calyptorhynchus.* The Mm. levator quadrati and sphenopterygoideus seen from the lateral side.

The Temporalis is a longer and narrower muscle which arises from a shallow depression upon the side wall of the skull below and behind the post-orbital process. The most posterior and inferior fibres take their origin from the side wall of the skull above the upper edge of the area of origin of the M. depressor mandibulae. The direction of the fasciculi is ventrad, rostrad and laterad, and, as the muscle passes toward its insertion, on to the upper edge of the mandible just behind the upper limit of the insertion of the M. massetericus, it grows thinner and its fasciculi are all inserted into a fine tendon which in turn is inserted on to the edge of the mandible.

The Quadrato-mandibularis muscle arises from the anterior surface of the ascending body of the quadrate bone and from the skull wall above and in front of it. It is a relatively thick sheet of fasciculi which pass ventrad with an inclination rostrad and laterad to be inserted into the upper edge and outer surface of the mandible under cover of the M. massetericus.

The Pterygoideus externus muscle is exceedingly well developed. It is a solid muscle of triangular outline and considerable thickness. It arises from the upper part of the surface of the strong bony int-orbital septum and from the under surface of the roof of the skull. It is, in

Cacatua and *Calyptorhynchus*, but not in *Polytelis* and other small parrakeets, incompletely divided into two heads. Of these the larger and more anterior arises from the septum, the other from the skull roof. The whole of the fasciculi are gathered into a short tape-like tendon which is inserted into a tubercle upon the inner surface of the mandible a little distance below the upper edge. This tubercle is the upper end of a ridge which marks the anterior limit of the insertion of the internal portion of the M. pterygoideus internus.

The Pterygoideus medius is a quite small, spindle-shaped muscle which arises from the wall of the skull immediately below the post-orbital process. Its fibres are gathered into a thread-like tendon inserted into a small tubercle developed at the anterior end of the ridge which is continued forward from the shelf on which the articular facet is placed. This tubercle is placed about the middle of the depth of the inner surface of the mandible a little way in front of the mid-point between the posterior end of the ramus and the posterior end of the gape.

A quite separate Pterygoideus posterior is developed. This is a small sheet of fibres which arise from the inferior edge of the anterior process of the quadrate bone and pass back to be inserted on to the ridge which passes back and down from the articular process of the mandible.

The Pterygoideus internus is a most massive muscle and must be described in two parts, "lateral" or internal and "medial" or external. The Pars lateralis arises by fleshy fibres from both the internal and external surfaces of the mandible. The areas of its origin are approximately similar to and opposite each other, and are confined to the posterior end (see Figs. 180–183, Pt. i). These fibres converge towards the inferior edge of the mandible as they pass ventrad and rostrad, and are there gathered on to a fascia upon the exposed surfaces of the muscle. The fascia finally becomes a short narrow tape, which is inserted into the antero-inferior spur of the palatine bone.

The Pars medialis is a mass of relatively short fibres which arise from the lateral surface of the os palatinum and pass ventrad and caudad to be inserted into an extensive area upon the inner surface of the mandible. Of these fibres, those which arise from the upper end of the palatine bone gather, with those behind them arising along the postero-superior margin, into a relatively thick fleshy strand which is inserted on to the inferior surface of the outstanding articular process of the mandible. In Fig. 182 the muscles are shown as though the mandible were transparent, and practically the whole of the inner surface of it over the area occupied by the parallel lines used to indicate the pars medialis of this muscle (Pt.i.s.) affords attachment to the muscle, whilst the portion of the palatine bone encroached upon by those lines indicates the area of its origin.

The Spheno-pterygoideus is another particularly massive muscle in these birds. It arises from the lateral wall of the skull, low down, below the otocrane and forward from this site to the posterior end of the int-orbital septum, where that fuses with the rostrum basisphenoidei. From this origin the fibres pass horizontally forward to be inserted into the full length of the pterygoid bone, and, passing beyond that bone anteriorly, into a sulcus along the postero-superior margin of the os palatinum in its upper half. This portion of the muscle, in its passage antero-laterally beyond the os pterygoideum, encloses that bone entirely.

The Levator quadrati muscle is a well developed bundle of fasciculi which arise from the side wall of the skull ventrally to the origin of the M. pterygoideus medius and pass ventrad with an inclination laterad and caudad to be inserted into the upper edge of the short anterior process of the os quadratum.

The Depressor mandibulae mandibularis is a short rounded bundle of fasciculi which take their origin from the skull immediately behind the posterior limit of the origin of the M. spheno-pterygoideus and pass directly ventrad to be inserted on to the upper surface of the inner part of the shelf behind the articular process of the mandible. In *Polytelis* and other small parrakeets I find that this muscle lies horizontally, and that its fibres pass from their origin directly forward to be inserted on to the inferior edge of the articular process itself. In the larger cockatoos the insertion of this muscle is immediately in front of the M. depressor mandibulae and median to it. As the two muscles pass downward to their respective insertions they converge, and one gains the initial impression that one is in the presence of two heads of the M. depressor mandibulae. This muscle is, however, innervated by a twig from that nerve which innervates the spheno-pterygoideus muscle, whilst the M. depressor mandibulae is, of course, innervated by the VIIth.

A feature wherein the M. pterygoideus externus of the parrots and cockatoos differs from that of all the rest of the Sauropsida, or for that matter from all the vertebrates other than the fishes, has deliberately not been mentioned in the above description because I have deemed it so important as to call for separate attention. It is that the muscle, at its origin, lies anteriorly to the optic nerve, and is to that extent pre-orbital. To my mind this is a feature of prime importance, because one of the strongest arguments against the acceptance of my contention, that the M. levator labii superioris of the sharks and rays is the homologue of the pterygoid group of muscles in the higher vertebrates, is the pre-orbital situation of the shark muscle.

Now, its situation deep to the second and third branches of the Vth nerve leaves us no doubt whatever that this muscle in the parrots is one of the pterygoid group. Its pre-orbital situation in these birds is proof positive that it is possible for a pterygoid muscle to have a pre-orbital origin. If we are able to accept as an accomplished fact the forward migration of a muscle post-orbital in other birds, there can no longer be any reason to doubt the possibility of a caudal migration of the same muscle in the progress of the modifications in masticatory mechanism which took place as between the fishes and the higher vertebrates.

Review.

Besides the birds whose musculature is described with more or less detail in the preceding pages, the following have been dissected: *Centropus, Hypotamidia, Halcyon, Struthidia, Nycticorax, Strepera, Anhinga, Corcorax, Anas* and three unidentified Eagles. In all, twenty-one birds have been dissected. In addition, a number of late embryos have been studied in serial sections.

This selection of birds covered, it is believed, a completely representative series, so that one is justified in believing that a composite picture based upon the common arrangement of the muscles in these, and omitting the isolated variations, may be regarded as presenting the typical avian arrangement.

Such a composite picture would reveal the following features:

THE MUSCLES OF MASTICATION.

These are divided into two groups, one superficial to the second and third branches of the fifth nerve, the other deep to those nerves. The superficial group would be divisible into massetericus, temporalis and quadratomandibularis muscles. Of these the first would be the most superficial and the last the deepest. The second group would be divisible into external, median, and internal pterygoid muscles and a spheno-pterygoid muscle.

The only superficial constrictor muscle innervated by the fifth nerve commonly present would be the Csv.1b. This would be found to be attached to the mandibular ramus deep to the line of insertion of the hyomandibularis muscle.

THE MUSCLES OF THE HYOID SEGMENT.

The constrictor colli fascialis dorsalis (Csd.2) would be found to be a relatively poorly developed muscle whose line of origin from the fascia dorsalis was placed just a little above the mid-lateral line.

The constrictor colli fascialis ventralis (Csv.2) would present itself in two portions, both arising from the post-articular lateral surface of the mandible and inserted, one beneath and slightly in advance of the other, into a mid-ventral tendinous intersection beneath the larynx or just in front of it.

The interhyoideus muscle would be found to arise just in front of the last two muscles and to pass forward and mediad to an insertion into the body of the hyoid or the hyoid cornu just behind it.

The depressor mandibulae muscle would be found to be comparable to the pars cephalognathica only of the reptiles.

THE MUSCLES INNERVATED BY THE NINTH NERVE.

The M. hyomandibularis would be found to arise from the hinder end of the hyoid cornu and to be inserted into the inner surface of the mandible, superficially to the posterior portion of the Csv.1b. It would also be found to be superficial to the Csv.1a when that muscle is present, and this extending so far forward.

The M. geniohyoideus arises from the lateral aspect of the fore end of the hyoid cornu and is inserted into the fibrous tissue of the ventrum of the tongue.

The M. interceratohyoideus lies deep to the Csv.2. It arises from one cornu and is inserted into a median raphe in which its fibres meet their antimeres. In certain birds, e.g. *Dromaeus*, this muscle is divided into two portions.

A M. thyrohyoideus is present in some birds, in others, apparently, its place is taken by the sterno-pharyngeal muscles.

So much, then, for what may be regarded as the typical arrangement of the avian cephalic muscles, but the departures from this "norm" are not without interest.

A typical M. Csv.1a appears to be present in *Eurystomus*.

In the cormorants, *Phalacrocorax* and *Anhinga*, and in some other birds, not so closely related but with equally long and narrow beaks, e.g. *Nycticorax* (Fig. 185) there is no deep layer to the Csv.2 and the anterior fibres of the superficial layer are woven through those of the opposite side, so that they appear to be woven through the posterior fibres of the Csv.1 (Fig. 185) and to be continued on to an insertion into the mandible deep to the M. hyomandibularis. In these forms one also notes that the Csv.1 is more extensive than is usual.

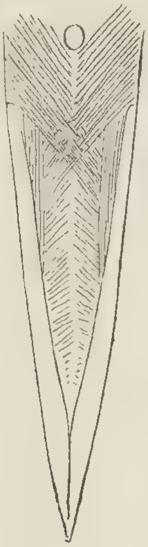


Fig. 185.—*Nycticorax*. The ventral superficial muscles.

It has not been possible to determine the limits of the Csv.2 and Csv.1 in these birds by the experimental method, but it is improbable that the Csv.2 fibres are really continued forward and across the mid-line. In *Eurystomus* the M. Csv.2 resembles one only of the two layers commonly present.

The variations in the muscles of mastication though (except in the parrots and their allies) never very extreme have, as a matter of fact, provided the means to the identification of the several muscles in the group. For it was only the occasional complete definition of one or more of the members of the group in various birds, which permitted the definition of the muscles in those birds in which the various muscles were more or less intimately fused.

COMPARISON WITH THE MUSCLES OF THE REPTILES.

It has been possible to recognize all the main divisions of the masticatory muscles found in the reptiles. The M. retractor anguli oris alone is missing. It will be remembered that it was not present in those reptiles in which the covering of the face region was rigid. That it should not be present in the birds is peculiar; they have, covering the face, a skin which is freely movable upon the deep fascia. Reviewing the reptilian muscles, it was suggested that the M. retractor anguli oris might, perhaps, be that portion of the temporo-masseteric muscle which, in the Bony Fishes and in the tadpole of the frogs, functions as a depressor labii superioris. If that should be the fact, then it is further suggested that its absence from the Aves might be explained on the assumption that they have been evolved from forms with rigid face covering.

Although a Csv.1a has been identified in the Dollar Bird, *Eurystomus*, it is not quite certain that this is not merely an anterior portion of the Csv.1b. The reason for the identification adopted is: it was found that in the generality of the birds, when the Csv.1b is continued far forward, its fasciculi were not continuous from side to side but were inserted, in the typical manner, into a median raphe. On the other hand the anterior fibres of the Csv.1b in *Eurystomus* itself are uninterrupted in the mid-line.

There is, however, still another interpretation to be placed upon the whole muscle in the Aves. There is no doubt that this muscle is inserted more dorsally than is the Csv.1b in the Reptilia, and in view of the fact that in some of those the Csv.1a fibres were interrupted at the mid-line, it is not entirely unreasonable to suggest that we have here only the Csv.1a. Though a possible alternative interpretation of the muscle, it is not adopted here.

All three of the reptilian muscles of the hyoid segment are constantly present in the Aves.

The division of the Csv.2 into two layers is of particular interest, as we shall find when we come to inquire into the origin of the posterior belly of the digastric muscle and the M. stylohyoideus in the Theria.

Turning now to the muscles innervated by the ninth nerve, we find that the question of their identity has been complicated by a further reduction in the branchial skeleton. At first sight it seems obvious that the muscle which, in the Aves, we have designated the M. hyomandibularis, must be completely homologous with the M. thyreomandibularis of the Reptilia. On the other hand there is quite a possibility that it is that muscle in complete fusion with one or more of the juxtaposed muscles.

It was this difficulty, and uncertainty in the identity of the avian muscles which caused me to give them designations other than those used in the work on the reptilian muscles.

THE LARYNX AND ITS MUSCLES.

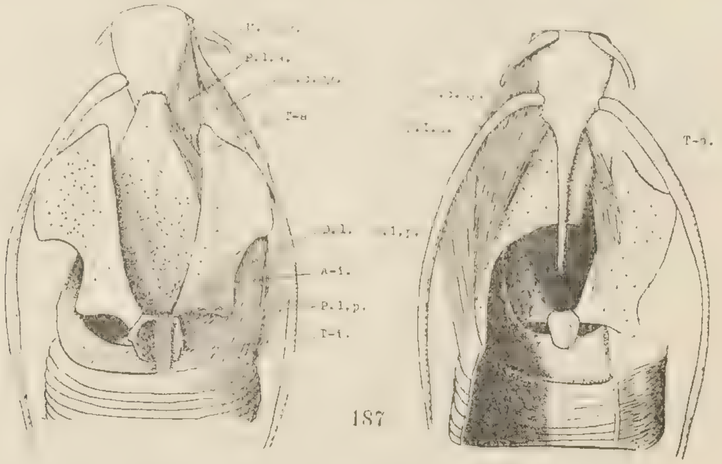
Dromaeus.

(Figs. 186–187.)

(*a*) *The Cartilages.*

The Thyroid is a complete hoop of cartilage which is split in the mid-line dorsally and rejoined by fibrous tissue. The ventral plate of the hoop is nearly three times as deep antero-posteriorly as the dorsal plate. As the use of the term "plate" probably implies, the hoop is dorso-ventrally flattened, and the lateral portions taper from the broad ventrum to the narrow dorsum. As indicated in the figures the dorsal plate is situated behind the caudal margin of the ventral plate. Anteriorly, the ventral plate is produced into a short spathulate process.

186



187

Fig. 186.—The larynx of *Dromaeus* in median sagittal section, semi-diagrammatic.
A., arytenoid cartilage; I.t., interthyroid cartilage; Th., thyroid cartilage.

Fig. 187.—*Dromaeus.* Dorsal and ventral view of the larynx, hyoid skeleton and related muscles.
A-i., M. arytenointerthyroideus; D.l., M. dilator laryngis; M.h.hy., M. hypohyalis; P.l.a., M. protractor laryngis anterior; P.l.p., M. protractor laryngis posterior; T.a., M. thyroarytenoideus (constrictor laryngis); T.i., M. thyrointerthyroideus.

The Interthyroid is a small plate of cartilage which is articulated to the anterior margin of the split ventral plate. The area of this articulation is increased by sinuation of the edge of the thyroid, so that the interthyroid is let into the sinuation. The base of the little cartilage is relatively thick at the place of articulation, and from this it tapers as it projects dorsad and rostrad.

The Arytenoids are two plates of cartilage, flattened in the coronal plane of the head, but with a concavity on the ventral surface and a thickened medial border which forms a ridge ventrally. Their shape is clearly shown in the figures. They articulate with the antero-lateral corners of the interthyroid.

(*b*) *The Muscles.*

(i) *The muscles moving the larynx as a whole.*—It will have been obvious that there are certain of the muscles which are innervated by the ninth nerve which must act to carry the larynx to and fro with the hyoid apparatus. In addition to those, there are several small muscles which act to move the larynx in relation to the hyoid skeleton.

The M. protractor laryngei anterior arises from the dorsal surface of the lateral edge of the hyoid body in front of the larynx, and is inserted into the lateral curve of the ventral plate of the thyroid.

The M. protractor laryngei posterior arises from the hyoid cornu, along a length which is placed anteriorly to the posterior end of the larynx, and is inserted into the lateral curve of the ventral plate of the thyroid behind the line of insertion of the last muscle.

The M. abductor cornu hyoidei is an adjuvant to the last muscle. It arises from the ventral surface of the lateral edge of the anterior end of the hyoid body, below the area of origin of the M. protractor laryngei anterior, and is inserted along the outer and dorsal surfaces of the anterior end of the hyoid cornu. Acting alone, it would abduct the cornu but in conjunction with the M. protractor laryngei posterior it would ensure that that muscle pulled the larynx forward instead of merely abducting the cornu.

Attached to either side of the ventral surface of the anterior tip of the hyoid body there are two little rods of cartilage. These have been provisionally designated hypohyals. From each of them there arises a small sheet of muscle fibres which pass mediad and rostrad to be inserted into the deep surface of the thick mucosa of the under side of the anterior end of the tongue. The anterior end of the hyoid lies in the butt of the tongue. This muscle can only function to keep the hyoid in position relative to the ventral mucosa.

(ii) *The Intrinsic Muscles of the Larynx.*—The M. thyro-arytenoideus arises from the dorsal edge and lateral surface of the anterior portion of the thyroid cartilage and runs caudad and laterally to be inserted on to the arytenoid cartilage along a narrow area on the ventral surface close to the medial edge.

The M. aryteno-interhyoideus arises from the dorsal surface of the arytenoid cartilage over an area towards its posterior end. The fibres converge to be inserted into the edge and half the anterior surface of the interhyoid.

These two muscles, acting together, act as a constrictor laryngei.

The M. dilator laryngei arises from the whole of the ventral surface of the arytenoid cartilage not occupied by the last muscle, and is inserted on to the dorsal plate and contiguous surface of the postero-lateral part of the curve of the thyroid cartilage.

The M. thyro-interthyroideus arises from a small area alongside the fibrous junction of the two halves of the thyroid cartilage and is inserted into the posterior surface of the interthyroid cartilage close to the articulating base.

General Discussion.

The larynges of a number of other birds were dissected, but the Emu was selected for detailed description because its peculiar arytenoid cartilage has caused the almost complete separation of the Mm. aryteno-hyoideus and dilator laryngei and permits their clear description.

In the great majority of the birds the arytenoid cartilage presents its surfaces medially and laterally. The dorsal edge is usually convex whilst the ventral is straight, the cartilage is plate-like and curved, with the convexity laterally placed. All the intrinsic muscles take their origin from, or are inserted on, this surface, covering it completely.

In most cases the superficial muscles are the two constrictors, the aryteno-interhyoideus being placed medially to the other. The dilator is usually covered by these. The only departure of importance from the arrangement of the muscles as seen in the Emu is that it is not uncommon for the more superficial fibres of the dilator muscle to be continuous with those of the muscle of the other side, crossing behind the interhyoideus cartilage and superficially to the little thyro-interhyoideus muscle.

The laryngeal skeleton in all the examples examined presented the same cartilages as in the Emu. In several instances it was found that the interhyoideus cartilage was interposed between the two arms of the thyroid separating them completely. In not a few birds this little cartilage was ossified. No ossification was observed in any of the other cartilages.

SUMMARY AND REVIEW OF SAUROPSIDAN MUSCLES.*

THE MUSCLES OF THE MANDIBULAR SEGMENT.

Two ventral superficial constrictors are constantly present. The M. submentalis (Csv.1a) lies far forward between the mandibular rami; it may be completely araphic so that its fibres extend uninterruptedly from one side to the other, as in the crocodiles. This is probably the primitive form of the muscle, since it resembles that of the fishes and amphibians, but if we are correct in regarding the raphic form as completely homologous with it, then this latter becomes the more important for our future studies, because there is no araphic muscle between the jaws of the Therians. In this connection an important feature of its location is that it always lies more deeply than the M. intermandibularis. Though, of course, the Ophidian muscle is not ancestral to any in the Theria, the form of the submentalis in the Snakes is of particular interest. It presents the extreme modification of the raphic form of the muscle, and the fact that the muscle has taken an almost antero-posterior direction in these reptiles must be accepted as evidence that such a modification was not an impossibility in the Theria. It is also important to recall that the M. submentalis is innervated by a branch of the fifth nerve independently of the M. intermandibularis.

The M. intermandibularis (Csv.1b) presents a division into anterior and posterior portions in some reptiles, but there is not the constancy in this subdivision that there is in the subdivision of the Csv.1 sheet as a whole, that is into Mm. submentalis and intermandibularis. Further than this the manner of this division of the M. intermandibularis is not one which may be regarded as inherited from the fishes or amphibians, but, rather, it should be regarded as a peculiar specialization in those reptiles in which it appears. This is important, because it might well be that if this subdivision of the M. intermandibularis had to be regarded as an inherited feature carried down from the elasmobranch fishes, then the expectation would be that such a feature would be portion of a muscular pattern so firmly established in the course of evolution that it should be looked for in further evolutionary changes in the Theria.

There is no doubt that the posterior of the portions of the M. intermandibularis in the majority of the Lacertilia closely resembles the posterior portion of the muscle in the Selachii. Lightoller, whose reptilian examples all presented this division of the muscle, designated the posterior portion " pars extramandibularis ", which term he had also applied to the posterior portion in the Selachians. This pars extramandibularis, however, is found only amongst the Lacertilia and in *Sphenodon*. Study of the development of several Lacertilians (*Physignathus*, *Tiliqua*, *Lygosoma*, *Varanus* and *Diporopherus*) reveals that the intermandibular muscle develops as a single sheet attached on each side to the medial face of the mandible throughout its length. Later, as the M. pterygoideus internus increases in bulk and extends its area of attachment below the posterior end of the mandible and then up over its external surface, the origin of the posterior portion of the M. intermandibularis is carried with it. This extramandibular origin for the muscle is, then, a peculiar, individual, ontogenetic and secondary character, of no phylogenetic significance.

THE MUSCLES OF MASTICATION.

Of particular interest was the discovery of most of the muscles of this group which were found in the Anura. The persistence of this pattern, of which we can now recognize some indication amongst the Selachian representatives, a further progress in certain of the bony fishes, and the very definite inception in the Urodela, must surely mean that it had by this time become a fixed pattern in the arrangement of the vertebrate muscles of mastication. We anticipate finding, at least, the main features of this pattern preserved in the Therian arrangement.

---

* The avian conditions have been compared with the reptilian on the previous pages and in the following review they will not be included.

The M. retractor anguli oris of certain of the reptiles may be simply an individual peculiarity. On the other hand it must be recognized that it is not without fairly close resemblance to the protractor labii superioris of the bony fishes and of the anuran tadpole. In all these it is a superficial portion of the temporo-masseteric mass. It is, therefore, just possible that it is in reality the complete homologue of that muscle ; beyond question it is completely analogous, but, though its derivation is the same, or at least very similar, it may yet be only a parallelism and not an homology.

THE MUSCLES OF THE HYOID SEGMENT.

The Superficial Constrictor (Csv.2).—Neglecting, for the moment, the anterior portion of this, which, as in the Amphibia, has been modified to act as a post-articular levator mandibulae, this sheet presents a fascicular continuum from the mid-dorsal to the mid-ventral line. In some reptiles the sheet is in two layers and the fibres of the deeper layer swing forward below the ramus of the lower jaw and extend some distance before being inserted into the superficial fascia superficially to the Csv.1b. The question arises in connection with these fibres, as to whether they are not a pars notognathica of the M. depressor mandibulae whose insertion has been transferred to the ventral fascia.

Behind the Cs.2 there is commonly an extensive superficial constrictor which is innervated by spinal nerves. In some reptiles the line of partition between the " M. Constrictor Colli Facialis " and the " M. Constrictor Colli Spinalis " is quite definite. In other forms it is impossible, by dissection, to define these muscles, one from the other. Experimental work, however, demonstrates that there is no portion of the two muscles with dual motor innervation.

The M. Depressor Mandibulae.—Lightoller's designations, partes cephalognathica and notognathica, have been used again for the divisions of this muscle, but his homologies for the two parts are not unreservedly accepted. The majority of the reptiles have both portions of the muscle well developed, but a large minority have only the pars cephalognathica. Certain of the Lacertilia which have only the pars cephalognathica present that division of the Cs.2 into two layers, and Lightoller has suggested that the deeper layer is the pars notognathica of this muscle, with a transferred insertion. The suggestion appears entirely reasonable. It is not uncommon for the pars notognathica to lie deep to the Cs.2 at its insertion. Whether this be the correct interpretation of this deeper portion of the Cs.2 or not, it is of particular interest to be able to record, quite definitely, that a portion of the superficial facial constrictor sheet has shown itself capable of taking up an almost antero-posterior direction. Such a modification, and such an extension forward of this sheet in a reptile prepares the way to the recognition of part of the sheet in the Theria.

With reference to the derivation of the pars cephalognathica, the discussion on the homology of the muscle in the Amphibia will apply equally to that of the Reptilia.

The M. interhyoideus.—This muscle has been recognized in the majority of the reptiles studied. Peculiarly, it is not present in either of the two Lacertilians studied by Lightoller (1939), although well developed in some other lizards. Its absence from *Tiliqua* and *Varanus* associated with the peculiar pars notognathica suggested, at once, that this latter was the M. interhyoideus. As against that identification it is to be remarked that the M. interhyoideus in the remainder of the Sauropsida arises further forward (from the angle of the jaw, Lacertilia, *Sphenodon* and Aves, or from the ceratohyoid, Chelonians) and is always inserted deep to the superficial sheets. The Crocodilia are peculiar, amongst the Reptiles, in that they have the primitive, expanded form of the muscle, arising and inserted deep to the superficial Cs.2.

THE MUSCLES INNERVATED BY THE NINTH NERVE.

It is not intended to review these muscles at length ; they have been introduced here only to stress the fact that experimental investigation failed to demonstrate any fifth nerve motor supply to the superficial longitudinal hyomandibular muscles. This work was carried out with *Tiliqua*, *Varanus*, *Chelodina* and *Gallus*. In every instance motor response to fifth nerve stimulation was obtained from the Csv.1b, and Csv.1a, if present, but none from the longitudinal muscle.

The importance of these observations will become apparent when we are discussing the homologies of the Digastric muscle.

REVIEW OF THE SAURIAN MUSCLES.

This review, originally written before the Therian work was commenced, has been rewritten because it was felt that the features which have been deemed of particular significance in their bearing on the interpretation of the Therian muscles should be drawn attention to at this stage of my work.

Unlike all the other reviews of the previous sections this one looks ahead instead of only backwards.

THE MUSCLES OF THE MANDIBULAR SEGMENT.

Probably one of the most interesting and important results of the investigation of the muscles of the Reptilia has been the discovery that the M. submentalis is very constantly present. This muscle first made its appearance in the Selachii, where it was recognizable, in some forms only, as an anterior portion of the Csv.1 only in that its fibres were araphic. Throughout the Bony Fishes the muscle was found to be of very constant occurrence and always to lie deeply to the rest of the Csv.1. Again, in the amphibians, though but poorly developed in many instances, the muscle was very constantly present, its fibres were araphic, and it was situated deep to the remainder of the intermandibularis muscle. Here in the reptiles the muscle is always placed more deeply than the Csv.1b and also deep to the insertion of the ventral longitudinal muscles. Its fibres may be araphic or they may be inserted into a median raphe. They may run directly transversely or they may have a very marked caudal trend. This last feature is most marked in the Ophidians.

The M. intermandibularis does not present any division into anterior and posterior portions except in certain of the Lacertilia. In these particular forms the growth of the M. pterygoideus internus around and on to the external surface of the mandible has carried the origin of the M. intermandibularis up on to the outer surface of the same bone. This portion was regarded by Lightoller (1939) as being homologous with the pars extramandibularis of the Selachian muscle, and he accordingly applied to it the same designation. Whilst the homology is, in all probability, just as Lightoller believed, the extramandibular origin of the muscle is quite adventitious, certainly in these Lacertilia, and probably also in the Selachians, so that a separate designation appears undesirable, because it may tend to give undue weight to a secondary character which is not of phylogenetic significance.

More important than this occasional extramandibular origin is, apparently, the occasional marked antero-posterior direction taken by the fasciculi of the muscle. This is not regarded as phylogenetically important because it has been handed on to the Theria directly, but because it is definite evidence that the muscle was capable of being modified to take up the direction we believe it to have taken in the Therians. There is no doubt whatever that it is the Csv.1b which in certain of the reptiles has been thus modified, therefore, when, in the Theria, we meet a muscle which on other grounds may be regarded as a modified Csv.1b, the fact that its fasciculi take a direction nearly parallel to the ventral longitudinal muscles cannot be counted as evidence against its recognition as the Csv.1b.

THE MUSCLES OF MASTICATION.

Throughout the Sauria these present themselves in the same two groups we became familiar with in the lower Vertebrata, and more especially in the Amphibia. One group in front of and deep to the second and third rami of the trigeminal nerve (or behind those nerves as a result of their area of origin having been extended back along the base of the skull and/or the pterygo-palatine arch) and the second group superficial to those nerves.

This constant division of the muscles of mastication cannot be regarded in any other way than as an inherited character of phylogenetic importance and it will be thus that we must regard it in our study of the muscles in the Therians.

There has been a tendency in the past to homologize the Therian muscles with those of the lower Tetrapoda on the evidence of their origin and relation to one another without reference to the nerves (see especially Brock, 1938). We have now followed the varying relations of the muscles to one another and their varying areas of origin throughout the whole of the lower Tetrapoda and have found these to have extended beyond the limits set by such a basis of classification. The wide variation in the Aves, remembering particularly the cockatoos, and the Reptilia, with special emphasis on the crocodilian conditions, was of such a graduated kind that we were always able to recognize, with confidence, not only the homologous groups but also the homologous muscles within those groups. Repeatedly the relations were such as would run counter to the suggested basis of classification of Brock.

It is, however, of interest to observe that this other basis of classification would be found to lead us, in the Therian studies, to the identification of the same two groups and individual muscles, as would the identification by reference to their relation to the nerves.*

MUSCLES OF THE HYOID SEGMENT.

Perhaps the most interesting and significant fact which emerges from the study of the hyoid muscles in the Saurians is that no settled plan of their relations to contiguous skeletal or muscular structures has been evolved. Amongst the component muscles, the pars cephalognathica of the M. depressor mandibulae is the only one which presents constancy of shape, origin, insertion and location generally. It was found that the fasciculi of the Csv.2 may run ventro-mediad without any obliquity, or they may take a marked rostrad inclination. They may be confined to the region of the neck behind the mandibles, or they may sweep forward between those bones for a considerable distance. They may be inserted in series with the Csv.1b or they may be inserted either deeply or superficially to that muscle. Finally the fasciculi may be arranged in a single or in a double layer. The muscle may arise as a continuous sheet from the dorsal fascia, or its anterior portion may arise more ventrally from other structures.

The M. interhyoideus may, apparently, be absent altogether or, in the alternative, be so modified and incorporated into other muscles that it is unrecognizable, or it may be well developed. When present it may arise from the ceratohyoid anywhere along its length, from the middle to the extreme distal tip, or being transferred to cranial structures, may arise from the otocrane, the quadrate or the post-articular piece of the mandible. It may be inserted superficially, in series with the Csv.1b and/or the Csv.2, into a mid-ventral raphe, or deeply to those muscles, either into a median raphe or to some part of the hyoid skeleton.

It is, moreover, of particular interest to observe that these variations are not characteristic of the several groups. Similar arrangements were observed in unrelated forms and dissimilarities in related.

In most instances it was not difficult to recognize the correlation of the observed arrangement of the muscles with an underlying modification of the skeletal structures or modification of the tongue. These characters in turn, however, were not, recognizably, of phylogenetic importance, but appeared to be individual variations.

The conclusions which one draws from these observations is that the Saurians have not yet reached stability of organization. They must still be in a plastic condition, and if this be so, then even more strongly must the same conclusion be expected to have applied to the Theriodontia.

If the musculature of the Theriodonts was in a plastic condition, then it would have readily been adapted to the profound modifications in the jaw articulation which took place in the evolution of Theria. It is of interest to note that in the course of those skeletal modifications the area of insertion of the only stable muscle, the pars cephalognathica, took up a completely new position. Thus was the way made clear for a complete rearrangement of the hyoid muscles.

Thus far we can carry our study of the comparative myology of the vertebrate head with a high degree of confidence that we have correctly identified the successive modifications of the primitive piscine muscles, but it is with far less confidence that we offer identifications of the components of the nine-twelve nerve-muscle associations.

Amongst the higher Tetrapoda the identification of these muscles is complicated by intracerebral nerve fasciculation (Kappers and others) and extracerebral nerve anastomoses, which have more or less completely obscured the original nerve-muscle pattern. The complications of this problem have recently been stated by Brock (1938). As she states, apparently identical muscles, functionally and topographically, " are quite distinct in origin and innervation ".

It is not proposed to discuss these muscles here ; that discussion will be taken up when we can include in it the mammalian muscles (see page 306).

---

* Lightoller's derivation of the M. pterygoideus from the levator maxillae superioris (L.1) of the Elasmobranchii has been discussed in a previous section. The evidence against the derivation appeared to be both positive and negative. Positive in that it appeared that one could definitely trace the evolution of the muscle from the levator labii superioris (add.) of the Selachians ; negative in that the M. pterygoideus as here derived appeared to be present in Bony Fishes as well as the M. levator maxillae superioris (the M. levator palatini) and that there appeared no explanation of the altered relation of the first ramus of the fifth nerve.

PART IV. THE THERIA.

The Superficial Facialis Musculature.
The Stylohyoideus Muscle.
The Posterior Digastric Muscle.
The Mandibular Muscles.
The Branchial and Hypobranchial Muscles.

In Part I of this work, dealing with the fishes, instead of describing the muscles of each species before proceeding to those of the next, each was described for the whole of each group. The object was to focus attention upon muscle groups and entities, rather than the musculature of the fishes themselves.

It appeared to the writer that the muscular systems of the vertebrata had been evolved, by adaptive modification, from some generalized fish type, and quite early it appeared that a deal of this adaptive modification might be observed in the conditions presented by the elasmobranchian cephalic musculature.

Therefore, the first portion of this work was devoted to establishing muscle groups and muscle entities, and at the same time, to an inquiry as to whether the varying complexity of the arrangement and modification of these, essentially similar, groups and entities in the process of functional adaptation in conformity with or response to skeletal changes within the fishes shed any light on their origin from a more generalized condition.

In that first part of the work the objective in view was deemed best attained by contrasting and comparing the muscles of the several segments, and it is believed that the comparisons made justified the belief that one could recognize, in the musculature of the mandibular and hyoid segments, certain of the muscles of the branchial segments, but more or less highly modified in adaptation to the changed form and/or function of the skeletal arches to which they are attached or otherwise related.

Passing to the Tetrapoda, it was decided that the study of the further modification of these muscles would be best carried out by observing their variation in relation to the whole of the muscles of each form studied. Having established the groups and entities, it became necessary to study their modification, and the range of their variations relative to other muscles and to the skeleton.

In this last section of the work there will be a return to the first method of study, firstly, because so many Therian types have already been fully described that it would be a work of supererogation to present the descriptions of a further series, and secondly because we have reached our goal. That goal has been to study the evolution of the musculature of the vertebrata with a view to determining the origin of those of the Theria, and especially that of the Mammalia. Clearly, then, it is not the function of this work to describe the wide variation of the Therian cephalic muscles, but simply to compare representative examples with those of the lower vertebrata.

Looking back, we recognize that in our passage from the fishes to the amphibians, it was the branchiate forms amongst the latter that presented us with the chain of beacons which assisted us in our passage along the stream of evolution. True, the chain was far from complete, many guiding lights appeared to be missing and others were hard to understand, but this chain of beacons made possible and profitable a passage which must have been much more difficult and much less satisfactory had we been called upon to pass directly from the fishes to the abranchiate amphibia.

Our further journey down the stream, from the amphibian territory to that of the Reptilia, was no more difficult than that from the fishes to the Amphibia. A surprising number of the guiding lights shone clearly, and with a good deal of confidence we have arrived at the farther confines of the Saurian territory, feeling that we have been able to chart the main current fairly correctly.

Briefly, it is believed that the evolution of the cephalic muscles, from the elasmobranchian type to the saurian, has been followed step by step and has been found to be relatively gradual and without markedly abrupt changes. It is now believed that the change from the saurian to the therian arrangement is really no more abrupt. The Mammalia have a remarkable and complex set of facial muscles which, at first sight, appear to be entirely new muscles, without anything to represent them in the lower forms.

It is, however, fairly satisfactorily demonstrable that this break in continuity of evolution is more apparent than real, and is due largely to failure to recognize the proper significance of the superficial facialis muscles of the Prototheria.

We find the same embryonic muscle plates in the Mammalia which we have become familiar with in the lower vertebrata, and related, of course, to the same segmental nerves. The similarity of the muscles developed from these muscle plates in all the forms already studied justifies the attitude adopted in this section. Broadly, this is that we have to seek detailed homologies amongst the individual muscles of groups whose homology, as groups, may be regarded as established.

It will be found that, in the Theria, the mandibular muscles are innervated by the branches of the fifth nerve, and, in their relation to one another, in a manner very similar to the divisions observed in the Reptilia and Aves, so that their interpretation in terms of the saurian musculature is not difficult. On the other hand, there the evidence bearing on the homology of certain of the muscles innervated by the seventh nerve is very indefinite.

In our approach to this question—the homologues in the Theria of the reptilian muscles innervated by the seventh nerve—it is necessary that we recognize at the outset that there has been a very marked change in the nature of the investment of the head, so that it is questionable as to how far one should press the inquiry. In what detail should one expect to be able to recognize homologies ?

In the introduction to this work it was stated that often we must expect to be able, at most, to indicate the derivation of muscles rather than their complete homologies. This appears to apply particularly to the muscles under discussion. In precisely the same way that it was contended that an homologue of the levator rostri could not be found in a fish without a rostrum, or a protractor labii superioris in a fish without a protractile upper lip, so the homologues of the facial muscles of the Theria, with their flexible skin and loose subcutaneous tissues, should not be expected in the Sauria, with their rigid head coverings.

This, however, does not debar us from speculating as to whether the muscles of the neck and throat in the Reptilia may not have provided the facial muscles of the Theria, and then seeking confirmation or correction of the idea by study of the distribution of the muscles derived from the hyoid muscle plate.

Although the cephalic musculature of a number of the Eutheria and of the Prototheria has been well described by previous workers, the writer's approach to the Therian musculature has been by actual dissections and serial sections of the embryonic material. This laborious course was decided upon for two reasons : firstly, actual familiarity with the structures was known, from experience, to be indispensable to their proper understanding, and, secondly, it was desired to preserve a point of view which had been steadily and deliberately built up by and during the compilation of the work as far as it had gone at this point.

Until I had almost completed my survey of the cephalic muscles of the lower vertebrata I refrained from study of the therian muscles. It was desired to approach these with as complete a knowledge as possible of those of the lower forms, so that they, the therian muscles, should appeal to me as modifications of those of the lower vertebrata. The desire was to avoid, as far as possible, interpreting the lower in terms of the higher.

This study of the therian muscles was carried to the stage of deciding their probable homologies or derivation before the work of previous investigators was consulted. This must not be taken as implying an expectation of errors of interpretation in the work of others ; it was simply carrying to its logical conclusion the policy, dictated by my desire to avoid the risk of interpreting the lower in terms of the higher, which had caused me to become familiar with the musculature of each group in turn, before studying that of the next higher group.

The development of the premandibular, mandibular, hyoid and branchial muscles differs in well known, important respects from that of other muscles. It has been generally agreed to regard these differences as being of fundamental importance and to regard these as "visceral" muscles, developed from visceral muscle plates, in contradistinction to the limb and body muscles, developed from " myotomes ".

There is reason to believe that it would probably be more correct to regard the " muscle plates " as the myotomes of their respective segments and to use the term visceral, when applied to these muscles, as a morphological term, having no particular genetic significance.

The Vertebrata did not spring "full formed" into existence; they have, undoubtedly, been evolved from some invertebrate form.

There is little reason to doubt that the mouth of the Gnathostomata and the branchial apparatus of the whole of the Vertebrata are completely new structures, developed in the course of the evolution from the invertebrate form. Further, it is highly probable that a number of body segments were impressed into the formation of these new structures. There can be no reasonable doubt that these segments were equipped with muscles developed from segmental myotomes, as in the rest of the segments.

We must, therefore, decide which of two alternatives is likely to be the more probable explanation of the origin of the musculature of the "visceral" arches. Either the original myotomes and their muscle were aborted, or their musculature was adapted to the new formation. To assume that muscular tissue already available was aborted and replaced by newly formed tissue of the same kind seems an altogether unnecessary exercise of the imagination. It is to be concluded that there is every probability that the so-called visceral muscle of these segments developed from modified myotomes. There is, therefore, no fundamental difference between these and the rest of the striped musculature of the body. Actually the modification is no greater than that of the muscles related to the ribs and sternum, and less than that of those related to the limb skeletons.

Edgeworth and others have recorded the fact that striped muscle, e.g. the constrictor pharyngis, may develop directly from the mesenchyme in the visceral wall or in the mesenchyme independently of any particular structures, e.g. the superficial facialis muscles of the Theria. These contributions constitute a definite demonstration that the muscles in question have developed by differentiation of the mesenchyme at a distance from myotome or muscle plate.

These, however, are not the only muscles to be so developed. It is not uncommon for muscular tissue of the limbs to make its appearance at a distance from the main body of the muscle buds of the limb. Not only is this so, but portions of the visceral muscle plates, in some instances, make their first appearance divorced from the rest of the plate, and make this appearance after the plate has been more or less well differentiated from the surrounding mesenchyme. Again, no muscle plate or myotome develops in the whole of its extent at the same time, always the plate increases in extent after the first portion has been differentiated.

There will, of course, be complete agreement that the plate which develops as a continuum is a single genetic entity, but if we are to regard as a new formation portions which are not continuous with the muscle plate or myotome, we must either make this distinction absolute, or we must make some purely arbitrary distinction as to what degree of separation shall be regarded as constituting the portion in question a new formation.

We may view the matter from a different angle: Earlier or later every myotome and muscle plate divides into its component muscles; this separation into parts does not take place at the same stage of differentiation in every species, nor, as a rule, does the plate divide into its component parts at the one time. First one and then another muscle anlage is split off from the main differentiating mass. It would appear that in some instances, e.g. limb buds in numerous lower Tetrapoda, this splitting takes place before there is sufficient differentiation to make the myoblasts recognizable from the surrounding mesenchyme. Stated generally, this is to say that there is reason to believe that groups of myoblasts may migrate from the original site of formation whilst still in morphologically undifferentiated condition. If this be not the explanation of the very early divisions of muscle plates which have been recorded, and which may be seen in examples of all the lower Tetrapoda, the only other interpretation is to regard perfectly normal muscles developed from these separate portions of the plates as "new formations" in the particular species in which they are found.

Such an explanation is, of course, completely untenable.

It follows that we remain within the bounds of complete reasonableness and, indeed, of probability when we suggest that those apparently new formations, the constrictores pharyngei and the Therian superficial facialis musculature, have been developed from their appropriate myotomes or muscle plates, but that their myoblasts had migrated far from the rest of the plate before differentiating. This interpretation has the advantage that it permits us to seek the origin of every muscle found in each group of Therians in that other group which may be regarded as presenting an approach to the ancestral form of the group under study.

To one who has observed the remarkable plasticity and adaptability of muscle tissue in a very large variety of species and genera of all the groups of vertebrates, it is difficult to believe that there has ever, in the evolution of the vertebrate musculature, been the need of new muscle tissue to supplement that already existing. With so many and such wide extensions and adaptations in mind, one is quite unable to believe that isolated muscles and/or groups of muscles must be regarded as entirely new formations whilst all the rest are demonstrably varying arrangements of the same muscles and muscle derivatives.

THE SUPERFICIAL FACIALIS MUSCULATURE.

The superficial facialis musculature is discussed first for the single reason that it is the most superficial of the cephalic muscles in the Theria.

Huber (1930) says of the facialis, hyoid, musculature of the Monotremes (Figs. 188–189) that they " developed along their own line, on a ground plan which is distinctly different from the common marsupio-placentalian ground plan ". Whilst this is correct, it fails to impress the really significant feature of the Monotreme facialis musculature, which is that it has *no* ground plan.

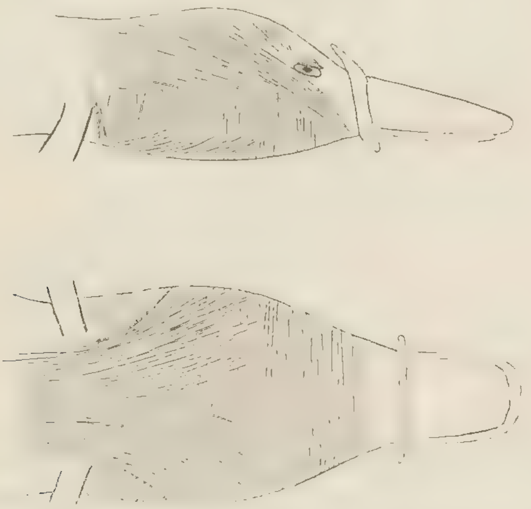


Fig. 188.—*Platypus.* The superficial facial muscles and the panniculus carnosus.

In several species amongst the lower Vertebrata we have observed a tendency of the superficial facialis musculature to extend dorsally. Compare, in this respect, *Varanus*, *Sphenodon*, *Chelodina* and *Ichthyophis* with other Reptiles and Amphibians. The observable extension of the superficial hyoid muscle sheet is in each of these instances associated with increased mobility of the skin and subintegumentary tissues. Whether the increased mobility, or, in other words, the extension of the muscle sheet, was a cause or a result it is not possible to decide, but there is in each of these instances a further factor which, probably, was causally contributive to the changed condition—the elongation and increased flexibility of the cervical region. It seems, at least, not improbable that this increased flexibility demanded and possibly caused increased mobility of the skin. If this be so then it may well have been that extension of the superficial muscle sheet was permitted by the increased freedom of the skin from the underlying fascia, and perhaps further conditioned by the need of control of the folding of the skin. This is the view which appeals to the writer as offering the most probable explanation of the observed facts.

It will be remembered that in the Holocephali we observed a somewhat similar modification of superficial muscles in association with increased mobility of superficial structures. In that instance it was the more superficial components of the trigeminal musculature which had been modified.

The ability of muscles to change and alter in conformity with altering related structures is strikingly illustrated by a number of isolated examples of peculiar muscles in individual species and genera in every group we have studied, as well as by the changes which are believed to have taken place and which have been regarded as fundamental to our understanding of the hyoid and mandibular musculature in terms of the branchial.

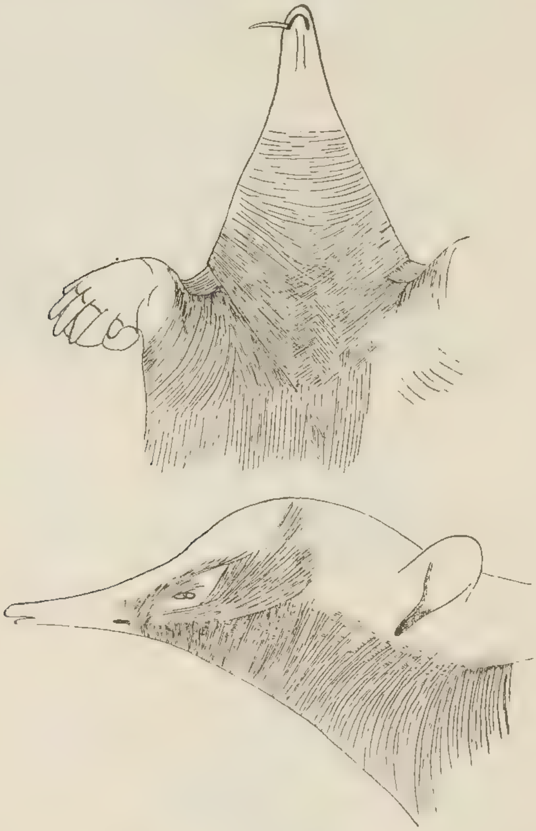


Fig. 189.—*Echidna.* The superficial facial muscles and the panniculus carnosus (after Ruge).

In the monotremes, except for the end of the snout, the whole head is covered by a flexible cuticle, and there is a wide range of movement of the neck and head upon the trunk. The need of orderly folding and control of the cuticle in harmony with the head and neck movements has, demonstrably, been met by the development of extensive sheets of muscle fibres.

Whilst the panniculus carnosus, originating from trunk myotomes, contributes in part to this nucho-cephalic sheet in its posterior part, the major portion of it is innervated by the seventh nerve and must be regarded as hyoid muscle.

Comparison of either of the monotremes, but especially the Platypus, with the lower forms mentioned above will, it is believed, reveal that the differences in the superficial hyoid muscle sheets in them are differences of degree rather than of kind.

Although previous workers have bestowed definite names on various parts of the hyoid muscle sheet in the monotremes, in actual fact no one of these is, even imperfectly, delimitated from another. It will be remembered that in a number of instances amongst the lower forms, it was found impossible to state definitely where the boundaries between components of the superficial constrictor sheets were ; they were defined by their origins and insertions only. Just in this same way, it is permissible to recognize component parts in the hyoid sheet of the monotremes.

Briefly, in the monotremes the superficial hyoid sheet of muscle fibres has spread forward and dorsad on to the side of the face and head, and various parts of it are functionally differentiated by their origins and/or insertions, but these are not anatomically differentiated by separation of their margins. The important thing to appreciate is that these muscles have not as yet been differentiated, though, in the light of the conditions in the marsupials and mammals, we may say that they are very definitely forecasted.

The origin of the facialis musculature of the Theria, and especially the superficial muscles of expression, have engaged the attention of several previous workers, and as a result there are now six outstanding explanations of their origin.

Gegenbauer was of the opinion that the whole of the superficial muscles were derived from a primitive cervico-facial platysma.

Ruge recognized that the primordial facial muscle plate divided into deep and superficial parts. The deep, he stated, gave rise to the stapedius, the stylohyoideus, the digastricus posterior and the platysma.

Huber investigated the question in greater detail than his predecessors and concluded that only the first three of the above muscles were derived from the deep portion of the plate. He was of the opinion, however, that the superficial sheet presented a primitive division into sphincter colli profundus and platysma, and that the whole of the retroauricular superficial facialis muscles were derived from the latter and the pre-auricular from the former division (Fig. 190).

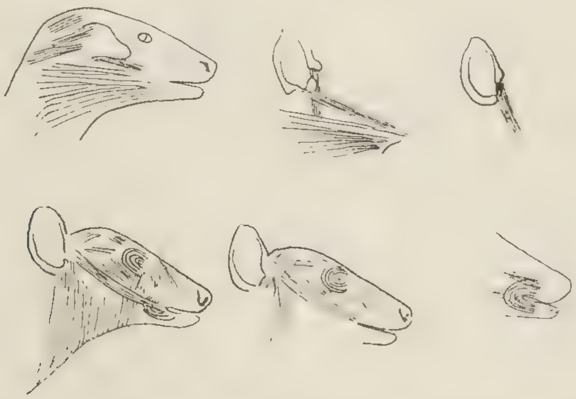


Fig. 190.—Huber's diagrammatic presentation of his theory of the origin of the various facial muscles. Those derived from the platysma, in the upper three drawings, those from the sphincter colli profundus in the lower.

Futamara (*vide* Lightoller) believed that he could demonstrate the division of the primitive cervico-facialis sheet into superficial and deep layers, that the deep yielded all the pre-auricular muscles, and the superficial, the platysma and the rest of the retro-auricular muscles. He thus combined the theories of Gegenbauer and of Huber.

Edgeworth believes that the whole of the facialis musculature of the Theria is an entirely new formation. He regards these muscles as being differentiated from the mesoderm *in situ*, *de novo*, and as not being portion of the facialis muscle plate with which we are familiar in the lower vertebrata. For Edgeworth only those muscles which lie deeply are survivals of the facialis musculature of the lower Vertebrata. It is not quite clear whether he regards the superficial muscles of those lower forms as having been lost, or whether he believes their anlagen are incorporated into the plate which gives rise to the deep muscles.

Lightoller has endeavoured to trace the evolution of the primitive branchial musculature of the Elasmobranchs through the changes in the hyoid and mandibular arches and then throughout the whole of the Vertebrata. Like all previous investigators except Edgeworth, he is of the opinion that the whole of the facialis musculature of the Theria has been inherited from the lower animals. Lightoller's approach to the subject has been very similar to my own, and I had the very good fortune of discussing the work with him as we both studied many identical species. There are many points on which we agree completely, but on others we agreed to differ. Lightoller's homologies are given in the following table.*

---

* The nomenclature of this work is given between brackets, where it differs from that of Lightoller.

	Elasmobranchii.	*Mammalia.*
Csd.1c.	Pars nucho-maxillaris (csd.1).	Notoplatysma
Csd.2a.	Pars epihyoidea (csd.2pr)	Portion of retro- and pre-auricular musculature
Csd.1c.	Pars mandibularis (csv.1b)	Sphincter colli profundus and trachelo-platysma
Csv.2a.	Pars interhyoidea (M. interhyoideus)	Stylohyoideus and digastricus posterior falsus
Csv.2b.	Pars inscriptionalis	Sphincter colli superficialis (the M. caninus)
L.2.	Levator hyoidei	Portion of the retro- and pre-auricular facialis musculature and digastricus posterior.

Of the above muscles the first and the third are, in the lower vertebrata, innervated by the fifth nerve, with a possibility by the seventh also in the Elasmobranchii.

The Stapedius muscle is derived by Lightoller from the M. stapedius of the crocodile.

Thus Gegenbauer, Ruge, Huber, Futamara, Edgeworth and Lightoller have all offered theories as to the origin of the facialis musculature. Of these, the simple explanation of Gegenbauer appears to state the probability as far as it *can* be stated in relation to the lower Vertebrata.

The therian facialis musculature includes superficial and deep components; the superficial have been classified as pre-auricular, retro-auricular, platysma and sphincter colli superficialis, and of the deep there are three separate muscles, the stapedius, the stylohyoideus and the posterior belly of the digastric.

In the Saurians the facialis musculature is made up of a continuous superficial sheet, a separated portion of this (the post-articular levator of the lower jaw) and a deep component, the M. interhyoideus. In the birds portion of the superficial sheet is in two layers.*

There is, therefore, except in the birds, no evidence of the existence of two layers in the superficial musculature in the hyoid segment of the lower Vertebrata, so that, apparently, the most we can say as to the origin of the therian superficial facial muscles, is that they were derived from the superficial constrictor sheet of the Reptilia and lower vertebrates generally.

There is no animal below the Theria existing today which is in possession of the primitive platysma and sphincter colli profundus postulated by Huber. It is hardly possible to recognize the condition in certain of the birds as presenting these two primitive sheets, although there is here definite evidence that already in the Sauria the single sheet had shown an ability to divide, at least partly, into two layers.

It is a fact that, with full knowledge of the muscles of the Eutheria, and searching for their equivalents, one may, by careful dissection, demonstrate portions of the superficial sheet of the Prototheria which conform to the requirements of portions of one or other of the two postulated sheets. This, however, is not evidence of the presence of the two sheets, but, rather, that all the superficialis muscles of the Eutheria have been derived from the single sheet in the lower forms. Futamara's (Lightoller) embryological findings are not evidence of the pre-existence of the two sheets, but are simply the ontogenetic differentiation of the primitive single sheet. The separation into deeper and more superficial layers has undoubtedly taken place and it was this separation which Futamara (Lightoller) regarded as of phylogenetic significance.

Lightoller's detailed correlation of the component parts of the Therian superficial and deep facialis musculature with the constrictors and levators of the Elasmobranchiata lacks the evidence of the persistence of some of the fish muscles in the Amphibians and Saurians. Their reported reappearance in the Therians is, therefore, subject to grave suspicion.

Some of these instances must be discussed in more detail than others.

The Lacertilia are really highly specialized Saurians, and it is unfortunate that the abundance of lacertilian material should have led to their tacit acceptance as typical of the reptilian conditions. In the Lacertilia the growth of the pterygoid muscles below and then up on to the external surface of the jaw pushed the origin of the posterior portion of the M. intermandibularis dorsally and externally on to the mandibular ramus, producing a condition very similar to that present in the Elasmobranchs and, in them, brought about in very much the same way. Here, then, Lightoller recognized a pars (extra-) " mandibularis ". Although differentiated from the pars intermandibularis in the elasmobranchian examples only by its origin, this muscle had appealed to Lightoller as of marked importance by reason of the fact that it is innervated by the seventh nerve in its posterior part.

---

* In a general survey such as the present, it would only cloud the issue to take cognizance of muscles which are only occasionally present, such as the deep facial cerato-hyoideus-capitis of *Chelodina*.

Amongst the Amphibians, as amongst the Bony Fishes, there is no example of a pars extramandibularis, and amongst the Sauria the muscle is found only in certain Lacertilia. In all these animals there is no evidence that the posterior end of the intermandibular constrictor is innervated by the seventh nerve: always it appears to be innervated only by the fifth.*

This difficulty of the innervation of the muscle in the Reptilia was noted by Lightoller.

It is doubtful whether the pars (extra-) mandibularis was worthy of a distinctive name. In the reptiles its peculiar origin is an entirely secondary and adventitious result of the overgrowth of one of the muscles of mastication, in the Elasmobranchs it is probable that the forward migration of the hyoid skeleton forced the original floor of the mouth ventrad, and that the complete covering of the external surface of the ramus of the jaw by the muscles of mastication caused the origin of the posterior part of the M. intermandibularis to be transferred to the facial covering of the masticatory muscles. The question of the innervation of the pars extramandibularis in the Elasmobranchs will remain unsettled until decided by an appeal to experimental stimulation of the severed nerve trunks and roots. It will be remembered that, as noted by Lightoller, there is a very intimate communication between the roots and trunks of the fifth and seventh nerves in these fishes, so that there is a possibility that the hyomandibular nerve carries motor fibres of the fifth nerve as well as mixed fibres of the seventh to the M. intermandibularis and the skin between the jaws.

Even if it should prove that the pars extramandibularis in the Elasmobranchs is innervated by the seventh nerve, the absence of the muscle from the lower Tetrapoda, except the Lacertilia where it is innervated by the fifth nerve, renders it improbable that any muscle present in the Theria and innervated by the seventh nerve should be homologous with it.

This objection is further supported by the fact that there is no other instance of the reappearance in the Theria of an elasmobranchian muscle which cannot be traced through the intervening vertebrate classes.† In other words, it would be the one instance of complete discontinuity in the phylogenetic history of the Therian muscles of the head and neck.

It should also be remembered that the acceptance of the theory of the homology of the pars extramandibularis of the elasmobranchian Csv.1b with any component of the therian facialis musculature carries with it acceptance of a belief in the myotomic, or segmental, duality of the facialis musculature, in support of which there is no other evidence.

It is, therefore, to be concluded that there is not sufficient evidence to justify the acceptance of Lightoller's equation of the Csv.1b pars extramandibularis with the Mm. sphincter colli profundus and tracheloplatysma.

The same general line of argument applies against the proposal to regard the notoplatysma as the equivalent of the Csd.1. This muscle is not present in any one of the lower Tetrapoda, and, even if it be the fact that it is innervated by the seventh nerve in the Elasmobranchs, its complete absence from all these forms makes one doubt very much that it should reappear in the Theria.

It is believed that the variability of the situation and relative extent of the superficial facialis sheet of muscle amongst the Amphibia and Sauria justifies the belief that the Therian facialis superficial musculature is simply a further extension of that same variable sheet, and to such an extent that it is not possible to indicate, with any degree of confidence in one's identification, from which portion of the muscle sheet of the lower forms the various therian entities were derived.

The division of the facialis sheet of the Theria into deeper and more superficial layers is not novel to the Theria. In most birds this division is seen ventrally. It is not logical to regard this partial division in the birds as the starting-point of the therian condition, because the birds cannot be regarded as ancestral to the Theria.

The multiplicity of designs presented by the various mammals and marsupials in the arrangement of the superficial facialis muscles provides an added reason for believing that they have been derived from an undifferentiated sheet similar to that of the Prototherians. There is, moreover, reason to believe that the marsupials present a more primitive condition than the mammals, reflecting, perhaps, the origin of some of the component muscles. Particularly, in this connection, we may single out the M. detrahens aureum of the wallaby (Fig. 191) and other diprotodonts. This certainly looks like portion of the saurian constrictor colli facialis which has gained an attachment to the ear.

---

* In the Bony Fishes, of course, the posterior portion of the M. intermandibularis is fused with the anterior portion of the hyoid superficial constrictor to form the protractor hyoidei, and there is dual innervation of the resulting muscle.

† Lightoller was of the opinion that the M. interhyoideus (pars interhyoidea of his nomenclature) is rarely represented in the reptiles. Unfortunately the muscle happens to be unrecognizable in the three reptilian types he studied, but a reference to the previous pages will remind the reader that the muscle is present in the majority of the Sauria.

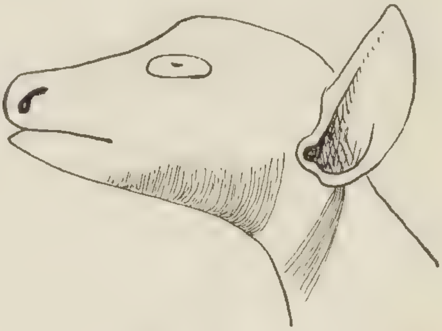


Fig. 191.—Wallaby. The M. detrahens aureum.

It seems reasonable to assume that there would have been a greater degree of similarity in the facialis muscle pattern in the mammals and marsupials, if the ancestral therian stock had already evolved a partially differentiated superficial facialis musculature. The basic pattern of this ancestral partial differentiation should, surely, be readily recognizable in all the Theria, if there had been one.

If, on the other hand, the primitive Theria had an undifferentiated sheet, similar to that of the Prototheria, then the wide degree of variation which we observe is completely understandable.

THE STYLOHYOIDEUS MUSCLE.

The whole of the arguments in favour of regarding this muscle as having been derived from the M. interhyoideus have been briefly and clearly stated by Lightoller (1939). With those views the writer is in complete agreement.

Edgeworth (1935) derives the posterior belly of the digastric muscle from the M. interhyoideus, but he states that in the higher Eutheria " . . . the interhyoideus separates into two parallel muscles, the stylohyoideus and the digastricus posterior . . ." This derivation of the muscles follows from his description of the early development of the hyoid muscle plate in the Mammalia. This, he states, " . . . separates into dorsal and ventral portions. The former is the primordium of the Levator hyoidei . . . the ventral portion is the interhyoideus."

This interpretation appears to assume the complete loss of the superficial components, and in the result he is forced to regard mammalian superficial facialis musculature as something quite new, and arising in the class without any precursor in the lower forms.

It appears, further, that Edgeworth assumes that when the myotome divides into a dorsal and a ventral part, the ventral must contain the anlagen of ventral muscles only, and the dorsal the dorsal anlagen only. This is a belief which, it seems, may easily be carried too far.

There are strong reasons for believing the M. depressor mandibulae of the Sauria to have been the precursor of the posterior belly of the M. digastricus. As will be pointed out later, its fibres have a tendency to extend beyond the mid-lateral line ventrally, and its origin to descend to a lower level than the origin of its precursor, the anterior fibres of the superficial hyoid constrictor. In this incomplete descent ventrad the muscle has come to lie across the mid-lateral line. If the digastricus posterior is derived from this muscle, then there has been a further descent, and an erstwhile dorsal muscle has become a ventral muscle. Not only is this so, but, if the homology is correct, from what we know of the ontogeny of the digastricus posterior in the Theria, the muscle plate was ventrally situated before it divided into its component parts.

In this connection it is noteworthy that the muscle which Edgeworth identifies as the levator hyoidei in the monotremes is placed wholly ventrally to the ventral limit of the similarly named muscle in the lower forms. It is placed ventrally to the quadrate and to the posterior end of Meckel's cartilage, and is derived from the primordium of the hyoid muscles *in this location* :

therefore, it is arguable that only the ventral moiety of the primordium is present at all, and that all the dorsal muscles of the hyoid segment have been lost. That is, of course, if the location of the primordial muscle plate at the time of its splitting be regarded as determining what muscles are developed from it.

THE POSTERIOR DIGASTRIC MUSCLE.

It is believed that this muscle is derived from the M. depressor mandibulae of the Sauria. It, therefore, becomes necessary to discuss briefly the probable origin of that muscle once again.

There is no apparent reason why we should doubt that the M. depressor mandibulae of the birds is completely homologous with that of the reptiles.

Throughout this work it has been assumed that every muscle in the higher forms has been derived from some muscle in the lower, and in the result there has been available to us the method of identification *per exclusionem.* In the present instance that method would be unsatisfactory; the M. digastricus posterior appears, at first sight, to be placed altogether too far ventrally to be the homologue of the remaining facial muscle, the M. depressor mandibulae, and also too deeply.

Let us consider first the point of origin of the muscle. In the Elasmobranchii the muscle arises from the side of the head at the level of the upper limit of the branchial muscles. In the bony fishes the origin is placed much more ventrally. In the Holocephali the dorsal limit of the muscle is variable, but is lower than in the majority of the Selachii. In the Dipnoi the muscle rises far toward the dorsum, perhaps, to some extent carried there by the dorsal situation of the vault of the branchial recess at the back of the skull. In the Euamphibia the origin of the depressor mandibulae is placed high up towards the dorsum of the posterior end of the head and neck, but in the reptiles one finds it arising lower down on the side of the head; the pars notognathica is commonly not developed. Lastly, in the birds, the pars notognathica is never present and the origin of the muscle is from the back of the skull behind the external auditory meatus.

An examination of the site of origin of the M. digastricus posterior in the Theria reveals that it is very closely just that of the M. depressor mandibulae in the birds and certain of the reptiles. The fact that it is so is, however, disguised somewhat by the increase in the size of the skull above and behind the otocrane. This has caused the area of skull behind the external auditory meatus to be overhung, so that the muscle appears to take its origin from a new situation altogether, whereas, as a matter of fact, there is but very little difference in the two locations. It would be foolish to deny that the site of origin of the therian muscle is not more ventrally situated than is that of the saurian; it is, but not nearly so much so as appears. Compared with the amount of migration of the site of origin of certain other muscles, particularly those of mastication, whose homology is unquestioned, the amount of migration of the site of the origin of this muscle is small and is not such as to constitute a reason why we should refuse to admit that the muscles are homologous.

Whilst the location of the origin of the muscle in the Theria calls for careful examination in view of its apparent novelty, the manner of its insertion presents nothing new. In several of the Reptilia, e.g. *Tiliqua* and *Varanus*, it was observed that portion of the Csv.2 extended almost to the mid-ventral line to gain an insertion into the superficial fascia. Whilst these were fasciculi of the pars notognathica and on that account, perhaps, not completely homologous with the therian muscle, which is regarded as having been derived from the pars cephalognathica, their ventral insertion bears very directly upon the question.

It will be remembered that in the Selachii the Csd.2 and Csv.2 formed a continuous sheet, in which we defined three parts by their origin, insertion, or relation to certain structures. In the Batoidei these parts were less easy to define. In the Chondrostei and in the Bony Fishes the identity of the three parts was almost completely lost, or at least profoundly modified.

In the Amphibia the M. depressor mandibulae fairly constantly presents a division into two parts, justifying a belief that it was derived from two muscles, but the contribution of the levator to this muscle was not a constant feature, though, possibly, that component was present in some forms. In the Sauria the muscle was found in two parts in some of the Lacertilia and Ophidia, but in other Reptilia and in the birds only the pars cephalognathica was present. Since the amphibian depressor was, very definitely, derived from superficially placed precursors, and since those form a continuous sheet in the Selachians and are profoundly modified in other ways in the bony fishes, the most that can be stated with confidence is that it was derived from the Csd.2 with a possible inclusion of the hyoid levator in some Urodela.

In the Reptilia, there is no evidence that a hyoid levator is ever present, at no time does the primordium of the M. depressor mandibulae show any division into deeper and more superficial layers. Indeed the separation into anterior and posterior parts, seen in some Lacertilia, is a relatively late happening. Although there is this definite splitting into partes noto- and cephalognathica in a number of lizards and snakes, the complete absence of such division from other lizards, from most, if not all, other reptiles, and from all the birds leads to the conclusion that the muscle is derived from one muscle only, and this conclusion is supported by the developmental history of the muscle.

The manner of innervation of the muscle in the Theria appears to have been regarded by previous observers as an obstacle to the homology accepted here. This does not appear as an obstacle to one who comes to the Theria from the lower Vertebrata. On the contrary, one finds complete conformity with the Saurian conditions. It is innervated by a post-auricular branch of the facial nerve.

One objection to regarding the M. depressor mandibulae of the lower Vertebrata as the homologue of the M. digastricus posterior of the Theria is the difficulty of accounting for the retro-auricular facialis muscles if they have not been derived from the depressor.

A critical examination of the varying areas of origin dorsally of the saurian M. constrictor colli facialis (Csd.2–Csv.2) will reveal that it is not uncommon for the origin of this muscle to lie superficially to the depressor.

Once the Csd.2 had obtained an origin superficially to, and overlying the depressor mandibulae the way was clear for it to invade the whole of the area occupied by the retro-auricular facialis muscles.

In both the Prototherians a muscle is found which is strictly comparable with the constrictor colli facialis, and which, indeed, has been designated constrictor colli by Huber. This takes its origin dorsally in a plane which is superficial to the situation of the M. depressor mandibulae.

It is concluded that there are no vital objections to regarding the M. digastricus posterior as having been derived from the M. depressor mandibulae of the lower Vertebrata.

It is, therefore, concluded that the M. digastricus posterior has been derived from the anterior fibres of the dorsal portion of the hyoid constrictor of the Elasmobranchii, for these alone are deemed to have contributed to the formation of the M. depressor mandibulae of the Saurians.

THE MANDIBULAR MUSCLES.

In order to maintain continuity of discussion the derivation of the M. digastricus anterior will be considered next.

The majority of workers have, in the past, derived this muscle from the M. mylohyoideus, the M. intermandibularis of this work. The latest review of the question is that of Lightoller who would derive the muscle in part from the intermandibularis and in part from the ventral longitudinal muscles. In this latter he is in agreement with the work of Rouvier (1906) and of Toldt (1907).

The ventral longitudinal muscles are innervated by spinal nerves, whilst the anterior belly of the M. digastricus is innervated by the fifth nerve only. Lightoller states: " . . . the lateral fibres of the ventral longitudinal muscle are pierced and apparently innervated by the N. mylohyoideus " and refers to his own observations to that effect in *Tiliqua*, and to the work of Chaine and Rouvier.

I have been able to confirm the observation in *Tiliqua* and have found the same distribution of the nerve in *Varanus* and in *Chelodina*. However, experimental stimulation of the distal and of the severed nerve fails to cause contraction of the longitudinal muscles in any one of the three forms; nor is there any contraction of the longitudinal muscles on stimulation of the nerve in the common fowl.

It is concluded that the twigs of the fifth nerve which reach the longitudinal muscles do not carry any motor fibres.

Perhaps the way to a proper understanding of this muscle has been obscured by a failure to realize that it is the Csv.1a portion, alone, of the amphibian and saurian mylohyoid muscle which is represented by the therian M. mylohyoideus.

This—submentalis—muscle first makes its appearance in the Elasmobranchs as an araphic portion of the Csv.1. In those fish it is placed on the same plane as the rest of the muscle. The M. submentalis is commonly well defined in Bony Fishes, but is variable in its relation to the insertion of the longitudinal muscles and to the posterior portion of the Csv.1 itself. In some species it is superficial, in others deep to these other muscles.In the Amphibia the submentalis is present in Urodela and Anura, but absent from the Coecilians and Dipnoi. It always lies deep to the plane of the M. intermandibularis, mylohyoideus of authors generally. Throughout the Reptilia there is an anterior part of the intermandibularis cleanly separated from the rest of the muscle and always placed dorsally, deeply, to it. The fibres of this reptilian M. submentalis may be araphic and directly transverse in their direction, or they may be inserted into a median raphe and have a direction diagonally posteriad and mediad, from their origin far forward on the inner side of the mandible. In most of the birds the Csv.1 is not differentiated into anterior and posterior parts in any way ; the submentalis muscle is not present.

The deeper situation of the anterior part of the Csv.1 in the Lacertilia led the writer to designate it the " pars profunda " until the araphic form was met in the Crocodilia and the true character of the muscle was recognized.

The situation of the M. submentalis is quite comparable with that of the Therian M. mylohyoideus, whereas the M. intermandibularis lies in a more ventral superficial plane.

The presence of this deeper portion of the M. intermandibularis in the reptiles appears to have been completely overlooked by previous workers.

Once we have recognized that this variable muscle was present in the Reptilia we are at liberty to assume that it was also present in the primitive mammal and it is easier to believe that it gave rise to the M. mylohyoideus than it is to understand how the superficially placed M. intermandibularis came to occupy a situation deep to other muscles of the mandibular segment.

If this be the correct interpretation of the mylohyoideus, it remains to determine what has become of the main portion of the intermandibularis, and one very naturally turns to the only other muscle in the region innervated by the fifth nerve, the anterior belly of the digastric.

Viewed from the saurian aspect it appears highly probable that the intermandibularis is represented in the mammals by the anterior digastric. This appears a much more likely interpretation of the facts than would be the assumption that the intermandibularis has been aborted.

The comparison of the M. intermandibularis with a M. digastricus anterior in such a form as *Homo* must lead to the rejection of the homology proposed here, but that is, of course, the extreme modification of the muscle. The early condition in the process of adaptation is presented in the Cetaceans, amongst others. That of *Delphinus* is illustrated here (Fig. 192). Comparison of this with the Csv. of lower Tetrapoda, and especially in those forms (*Varanus*, *Sphenodon*, *Crocodilus*, *Chelodina* and *Dromaeus*) in which the fibres have a direction caudad and mediad, reveals at once that there is really very little difference between them. Even the firm insertion of the mammalian muscle into the hyoid is definitely foreshadowed by the binding of the mid-ventral raphe to the hyoid apparatus in a number of Saurians.

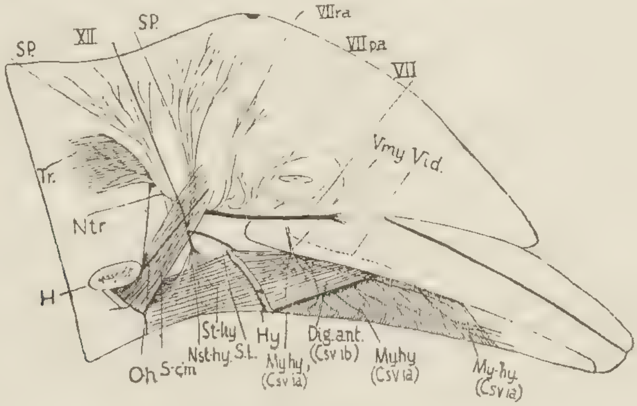


Fig. 192.—*Delphinus*.

Csv.1b, M. digastricus anterior ; H., humerus ; Hy., hyoid cornu ; Csv.1a, M. mylohyoideus ; N.st.-hy., the nerve to the M. stylohyoideus ; N.tr., the nerve to the M. trapezius from the cervical plexus ; O.h., M. occipitohumeralis ; S-c.m., M. sterno-cleido-mastoideus ; S.l., the superior laryngeal nerve ; Sp., sensorimotor nerves to the panniculus and dorsal trunk region from the cervical plexus ; Tr., M. trapezius ; V.i.d., the inferior dental nerve ; V.my., the myloid branch of the inferior dental nerve ; VII p-a., preauricular twigs of the facial nerve ; VII r-a., retroauricular twigs of the facial nerve. (From Kesteven, 1941*d*.)

The mammalian M. mylohyoideus presents itself in two layers in a number of species (*vide* Bertelli, 1927). It might appear that its two layers are homologous with the two layers of the Saurian Csv.1, the Csv.1a and Csv.1b. There is no doubt that this interpretation of the muscles is a completely admissible interpretation and there is no evidence to negate it completely.

On the other hand, if the two portions of the first ventral superficial constrictor have been so modified, we are forced to look to extramandibular muscles for the homologue of the M. digastricus anterior.

Since the only experimental work carried out to test the nature of the fifth innervation of the longitudinal muscles which have been homologized with the digastricus anterior has shown that innervation not to be motor, it is concluded that those muscles probably did not contribute to the formation of this. We are therefore left without any forerunner to the M. digastricus anterior in the lower tetrapods. But, inasmuch as the M. digastricus anterior has been demonstrated to be genetically a mandibular muscle (Edgeworth, 1935), we are constrained to return to the only mandibular muscles of this region in the lower Tetrapoda, and we are once more forced to look to the Csv.1b.

It is, of course, possible that only portion of the Csv.1b has been converted into the anterior digastric and that the remainder has contributed to the formation of the M. mylohyoideus. Against this, however, it must be pointed out that the line of origin of the digastric alone is in the situation of the line of the origin of the Csv.1b, whilst the line of origin of the mylohyoid is deep to that and is in the position of the line of origin of the Csv.1a.

THE MUSCLES OF MASTICATION.

The discussion of these muscles may be made very brief. There is no reason why we should not homologize the two groups of these muscles in the Theria with those we are familiar with in the lower Tetrapoda. This is, of course, in conformity with past practice. The origins and insertions satisfy the equations perfectly, as also do the relations to the branches of the fifth nerve.

THE BRANCHIAL AND HYPOBRANCHIAL MUSCLES.

Looking back over these muscles in the lower Vertebrata it appears as though there had been little congruence amongst them, but, if we omit from our review the muscles of occasional occurrence and tabulate those which may be regarded as characteristic of each group, it is found that there is a relatively high correspondence amongst them. This agreement is further brought out by the diagrammatic presentation of the muscles in Figs. 193 and 194.

The peculiar specialization of the Bony Fishes may be regarded as excluding them from the evolutionary history of the Tetrapoda, and we may, therefore, neglect them in the present discussion and pass from the Elasmobranchii direct to the Urodela.

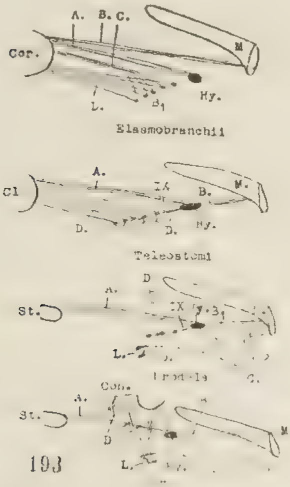
Comparing these we find that the continuous coraco-mandibularis muscle of the fishes has been replaced by a muscle interrupted at the hyoid arch. On the other hand there is present in the elasmobranchiate musculature a shorter coracohyoideus as well as the long muscle. Deep to this again there is the coracobranchialis communis, and all three are hypobranchial muscles and are innervated by the composite occipito-spinal "hypoglossal" nerve.

In the Urodeles the coracomandibularis may be regarded as having been cut off short at the hyoid, and the coracobranchialis communis as having lost its connection to the coracoid also. It will be remembered that the three elasmobranchian muscles are intimately fused for the greater part of their length, therefore the suggestion that the coracomandibularis and the hyomandibularis should have been modified in the Urodela as suggested involves a comparatively slight change. The fusion of the two muscles along their whole length instead of for part only is all that is called for.

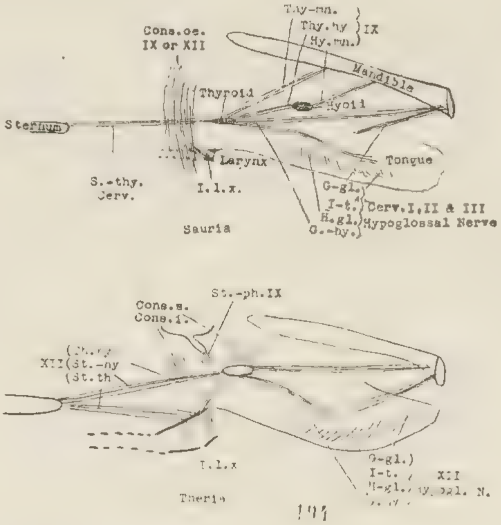
If further we assume that the coracobranchialis communis also became fused for a much greater length, its extension into the region of the tongue may be regarded as an easy step. The genioglossus may be regarded as a modification of the deep portion of the geniohyoideus.

It is not contended that any of these muscles is the homologue of any other, but it is believed that these hypobranchial spinal muscles of the Urodela are directly derived from those of the Elasmobranchii.

Whether this be the fact or not, it is of interest to note that the arrangement of the principal hypobranchial muscles of the Tetrapoda remains unchanged throughout the whole series. The pattern is slightly disguised amongst the Reptilia by the varying presence or absence, and varying relations, of certain muscles which lie ventrally to them.



193



194

Fig. 193.—Diagram of the branchial and hypobranchial muscles in the lower Tetrapoda. A., Mm. coracohyoideus, claviculohyoideus and sternohyoideus; B., Mm. coracomandibularis and geniohyoideus; C., Mm. genioglossus and hyoglossus; D, branchial muscles; L, larynx.

Fig. 194.—Diagram of the branchial and hypobranchial muscles of the Sauria and of the Theria. Cons.i. & Cons.s., the inferior and superior constrictor muscles of the pharynx; G.gl., M. genioglossus; G.hy., M. geniohyoideus; H.gl., M. hyoglossus; H.mn., M. hyomandibularis; I.l., intrinsic muscles of the larynx; I.t., intrinsic muscles of the tongue; St-hy., M. sternohyoideus; St.thy., M. sternothyroideus; Th.hy., M. thyrohyoideus; Th.mn., M. thyromandibularis; IX, X and XII, the nerves innervating the muscles.

Though it is possible to recognize the sternohyoideus and geniohyoideus in the great majority of the Tetrapoda, it is the fact that the muscles so identified are not always innervated by the same nerve. In the Lacertilia, there are two other muscles which pass from the hyoid apparatus to the mandible and one other which passes from the thyroid cartilage to the hyoid. These are longitudinal muscles and they are innervated by the glossopharyngeal nerve. In the birds, there is always a muscle which passes from the hyoid to the mandible, and not uncommonly this muscle is divided into a lateral shorter part and a medial which may extend right to the symphysis menti. It is functionally a geniohyoideus and has been so named in the body of this work. It also is innervated by the IXth nerve.

In the Theria, in addition to the sternohyoideus and geniohyoideus, there are sternothyroid and thyrohyoid muscles innervated by the glossopharyngeal nerve.

In all the Tetrapoda, there is a constrictor pharyngis, innervated by the vagus. In the Theria, the muscle is present in superior and inferior divisions.

Comparing the Anura and the Reptilia, one finds in the former three branchial muscles—craniohyoideus, craniolaryngeus and dorsolaryngeus—innervated by the Xth and/or IXth nerve. These might appear to be the forerunners of the three muscles which we have found in the Reptilia situated ventral to the hypobranchial muscles and innervated by the glossopharyngeal nerve.

Actually, however, these two trios have little in common to support such a suggestion. The amphibian muscles are demonstrably branchial, their development from typical branchial muscles, during the metamorphosis of the tadpole, is readily observed. The reptilian muscles, on the other hand, are developed from the same stroma as the typical hypobranchial muscles.

Edgeworth would regard their innervation by the IXth nerve as secondary, as also would he regard the glossopharyngeal innervation of the Avian geniohyoideus and hyomandibularis (branchiomandibularis).

This interpretation appears to be entirely reasonable, but it is suggested that the "secondary" character of the innervation may be more apparent than real. It is possible that the true explanation of their innervation is that their motor fibres have taken a shorter, new, intracranial course and issue with the IXth instead of with the rest of the Xth nerve.

That which is here suggested is the converse of the explanation of Straus and Howell (1936) for the innervation of the accessorius muscles by spinal nerves in the long-necked Ungulates. Their suggestion is that true accessorius fibres still innervate those muscles, but that they have taken a new intraspinal course and now issue with the cervical nerve fibres.

It is an interesting fact, probably not without significance, that, with the exception of the intrinsic muscles of the larynx, the branchial muscles throughout the whole of the Vertebrata are constrictor muscles. Even the interarcualia recti act to bring the branchial arches together and assist in the more perfect compaction of the branchial basket.

After the most careful study of these muscles in the extensive series of animals whose muscles have been described in the earlier parts of this work one can only record the impression that the evidence is not available on which to determine with confidence the origin of the branchial muscles in the higher Tetrapoda with any degree of exactitude.

Embryological evidence appears to indicate different segmental origins for apparently identical muscles in more than one instance.

The outstanding phenomenon in the changes in the branchial region as we have traced the muscles from fish to Theria has been the gradual reduction in the number of segments which have been carried forward from group to group. This reduction has obscured the sequence of inheritance so much that it is not always possible to determine which segments remain; much less is it possible to determine which muscles have persisted in the altered conditions observed.

It is concluded that the most one can say with confidence is that the vago-glossopharyngeal muscles, as a group, are homologous throughout the Vertebrata, but that owing to the possibility, if not the probability, of fasciculation of the nerves in this region, it is not possible to separate the muscles into vagus and glossopharyngeal groups.

Not only is this so, but there is reason to believe that certain of the muscles innervated by the glossopharyngeal nerve are really hypobranchial and not branchial in origin, as already stated.

The final conclusions of this part of the work are conveyed by the tabulation below. A reference to the earlier tables of similar kind, conveying the conclusions of each section will give the homologies, as the writer sees them, of the Therian muscles with those of each of the groups of the lower Tetrapoda.

	Hypobranchial Muscles Innervated by Nerves behind the Vagus		Branchial Muscles Innervated by the IXth and Xth Nerves.	
Elasmobranchii	Coracohyoideus	A		
	Coracomandibularis	B	Intrinsic branchial muscles	D
	Coracobranchialis communis	C		
Teleostei	Claviculohyoideus	A	Intrinsic branchial muscles	D
	Geniohyoideus	B		
Urodela	Abdominohyoideus	A	Intrinsic branchial muscles Intrinsic laryngeal muscles Constrictor pharyngis	D
	Geniohyoideus	B		
	Hyoglossus Genioglossus	C		
Anura	Abdominohyoideus	A	Tadpole Intrinsic Branchial muscles	D
	Hyoglossus	B	Adult Craniolaryngeus Craniohyoideus Dorsolaryngeus Intrinsic laryngeal muscles Constrictor pharyngis	D
	Hyoglossus Genioglossus	C		

	Hypobranchial Muscles Innervated by Nerves behind the Vagus		Branchial Muscles Innervated by the IXth and Xth Nerves	
Sauria	Sternothyroideus	A	Thyromandibularis Thyrohyoideus Hyomandibularis	B
	Geniohyoideus	B		
	Hyoglossus Genioglossus Intrinsic muscles of tongue	C	Intrinsic laryngeal muscles Constrictor pharyngis	D
Theria	Sternohyoideus Sternothyroideus Thyrohyoideus	A	Stylopharyngeus Constrictor pharyngis sup. Constrictor pharyngis inf. Intrinsic muscles of larynx	D
	Geniohyoideus	B		
	Hyoglossus Genioglossus Intrinsic muscles of tongue	C		

I have, in conclusion, to acknowledge gratefully the receipt of several grants from the Trustees of the Commonwealth Council of Scientific and Industrial Research, which have helped very materially to make this work possible.

POSTSCRIPT.

(Added 29th July, 1944.)

In this year of grace 1944, some five years after the work was finished, years packed full of civilian war work and away from microscope and scalpel, a critic has asked me what remains to be done to correct or confirm my conclusions. The reply seemed obvious to me. I have offered working theories only, and have proven nothing. The whole field needs covering again, not once but probably many times, before sufficient types and varieties of arrangement have been studied anatomically and embryologically, and sufficient evidence will have been amassed on which to establish a sound and completely satisfactory explanation of the evolution of the cephalic muscles and of the skull.

My critic then suggested that at least I should be able to indicate where I had wished more evidence had been available to me. That information, he thought, would be useful guidance and perhaps provide inspiration for future students.

I have, therefore, endeavoured to revive the mental atmosphere in which the work was done by reading it through. I have not succeeded, for my recollection is of a constantly recurring sense of frustration due to absence of conclusive evidence whilst the work was in progress. I feel that, had I been keeping notes with a view to compiling such a chapter as this, many more lines of research would have been suggested.

On pages 3 and 4, I discussed the constant association of segmental nerve and muscle-plate derivatives and offered an explanation of this constancy. It would be interesting to test both the explanation offered and the apparent exceptions. Examples of "heterogeneous" innervation are the branchial levators in Selachii (pp. 12–13), the protractor hyoidei in Teleostei (pp. 72–77) and also in certain constrictor colli muscles in the Sauria. The "explanation" could, it is believed, be tested in the manner suggested, the apparent examples of heterogeneous innervation, by stimulation of the motor nerves.

A careful study of the development of the mandibular muscles of the Selachii would yield interesting results. The study should be carried out with serial sections of the very early stages, and, of course, reconstruction from the sections. Actual three-dimensional vision of the structures is essential for their proper understanding. This study of early stages would need to be supplemented by actual dissection under high magnification of the earliest stages to which the method is applicable, and further dissections of later stages until the adult form is reached. I think that such a study would either confirm or correct my belief that the quadratomandibularis is derived from the primitive middle adductor, and the rest of the muscles of mastication from the primitive dorsal adductor.

In view of the many cranial and muscular similarities of the Chondrostei to the Selachii, suggesting comparatively recent divergence from the parent elasmobranchiate stock, a re-survey of the development of the branchial muscles would be interesting. It is possible that such a survey would lead to the recognition of evanescent traces of some of the missing elasmobranchian branchial muscles.

The history of the origin of the laryngeal and pharyngeal muscles in the Anura is still largely wrapped in mystery. I have no doubt that much could be learned by actual dissection of larger tadpoles. This problem would be most easily solved if the development of the muscles were studied backwards. Complete familiarity with adult form and disposition should be acquired first, then this condition should be seen in the youngest tadpole in which it is attained. Then would follow a search for successively earlier and earlier stages, perhaps ending with reconstructions of the earliest from serial sections. This work would be very tedious and difficult if attempted on ordinary small tadpoles, but some tadpoles (e.g. *Myxophyes* and one of the *Hyla* species) attain relatively monstrous size long before metamorphosis commences, and these are relatively easy to dissect.

Very naturally, I should like to see my theories relative to the correct interpretation of the fourth and sixth nerves tested in some way. Being neither an experimental embryologist nor a neurologist, I can make no suggestion as to how they might be tested.

I feel that full use has not yet been made of fossil skulls. Few, if any, of them have been studied by the application of our method of serial section and serial plate reconstruction. There is no reason to believe that even those encased in friable matrices, or coal, would not yield perfect sets of serial sections if carefully encased in a cement envelope, and if each section were firmly stuck to a glass slide with canada balsam before being cut from the block. Outline drawings of the bones, with sutures and small foramina carefully marked on them, could then be traced from both sides of each section on to sheets of blotting paper of appropriate thickness, and the whole assembled just as is done in the reconstruction of embryonic skulls. This method would be infinitely preferable to that of attempting to clean the bones *in situ* and/or " restoring " the unseen parts. In the reconstructed model, the whole skull, including the bones of palate, suspensarium, and jaw, could be handled and taken apart, in fact " disarticulated " if required.

In conclusion, having acted on his criticism, it is only right that I thank my son, Geoffrey L. Kesteven, for having given it.

INDEX.

A

PAGE

Amia, lower jaw .. 120
  skull .. 113
Amphibia, evidence of certain bones on the evolution of .. 232–236
  a new classification of .. 236
  phylogeny of .. 218–229
    evidence of the cephalic muscles 230–232
Amphibolurus .. 246
Amphiuma, laryngeal muscles .. 195
Anolis .. 246

B

Branchial arches in Elasmobranchii and Teleostei .. 64
  skeleton in Holocephali .. 57

C

Carcharias, skull .. 94
Cheiropterygium, evolution of .. 229
Chondrostei, skull .. 100
Coecilia, muscles of hyoid segment, synonymy .. 189
  mandibular muscles, synonymy .. 188

E

Ectopterygoid, identification of in the fishes .. 127
Eusthenopteron, lower jaw of .. 121

F

Fishes, phylogeny .. 128

H

Heterodontus, skull .. 97
Holocephali, branchial skeleton .. 57
Homology of certain cranial bones 232–236
Hyoid skeleton in *Physignathus* .. 244

I

Innervation of the eye muscles .. 91
Investigations, further, required .. 309

L

Lepidosteus skull .. 116
Lower jaw in Bony Fishes .. 120

M

Maxilla, evolution .. 125
  abranchiate Amphibians .. 171
  anuran tadpoles .. 143
Muscles, anuran tadpoles compared with those of Dipnoi and fishes .. 151
  aves compared with those of reptiles .. 287
    review of .. 286
  Batoidei, table of .. 36
  branchiate Amphibians .. 133
    review of .. 166
  Chondrostei, review of .. 56
  Dipnoi .. 134
  Heterodontus, table of .. 28
  Holocephali, review of .. 60–63

PAGE

Muscles—*continued.*
  Plagiostomi, review of .. 56
  Psephurus, table of .. 53
  pterygoideus, homology from fish to amphibia .. 191
  Reptilia, table of .. 237
  Saurian, comparative review of 292–293
  Sauropsidan, review and summary of .. 290–291
  Selachii, table of synonymy .. 15
  Teleostei .. 63
  urodele larva .. 115
Muscles of branchial segments in Neoceratodus .. 140
  hyoid segment in fishes and amphibians, review of .. 193
    in *Neoceratodus* .. 137
  larynx in Aves .. 288–290
  mastication in Aves .. 286
    in *Podargus* .. 279
Muscle homologies in Selachii, Teleostei, and amphibia, table of .. 135
  innervated by ninth nerve in *Eurystomus* .. 282
    in Aves .. 286
      Dromaeus .. 278
      Gallus .. 274
      Struthio .. 278
  synonymy of in *Accipenser* .. 54
    Holocephali .. 56
    Polydon .. 54
    Psephurus .. 54
  abdominohyoideus in *Amblystoma* .. 175
  adductor arcus palatini in Teleostei .. 75
    hyomandibulae in Teleostei .. 79
    operculi in Teleostei .. 79
  adductores arcuum branchialium in Chondrostei .. 53
  atlanto - epistropheo - hyoideus in Ophidia .. 267
  attrahens scapulae in axolotl .. 160
    Molge .. 179
  branchial in Theria .. 306–309
  branchial adductor in Batoidei .. 39
    Heterodontus .. 29
    Holocephali .. 57
    Selachii .. 13
    Teleostei .. 68
  branchial constrictor in Myxophyes tadpole .. 146, 148, 150–151
  branchial depressor in Batoidei .. 39
    Heterodontus .. 29
    Selachii .. 13
  branchial epiarcualis obliquus in Teleostei .. 67
  branchial and hyoid, serial homology of, in Batoidei .. 47
    Heterodontus .. 47
    Selachii .. 47
  branchial levator in Batoidei .. 38
    Chondrostei .. 53
    Heterodontus .. 29

PAGE
Muscles—*continued.*
Holocephali 57
Necturus 165
Neoceratodus 140
Selachii 12
Teleostei 65
branchial segment in Selachii 11
branchial subarcualia transversi in Batoidei 38
branchio-mandibularis in Teleostei .. 70
cephalo-dorso-pectoralis in Amphibia 169
cerato-hyoideus in *Dromaeus* .. 278
Struthio 278
cerato-hyoideus anterior in *Amblystoma* 173
Spelerpes 179
cerato-hyoideus-capitis in Chelonia .. 264
cerato-hyoideus internus in *Amblystoma* 173
cerato-thyroideus in *Dromaeus* .. 278
Struthio 278
chiasmique 141
claviculo-branchialis in *myxophyes* tadpoles 146
claviculo-hyoideus in *Amblystoma* .. 175
Axolotl 160
Neoceratodus 142
Teleostei 70
constrictor branchialis ventralia in *Myxophyes* tadpole .. 147, 149
constrictor colli facialis 262
constrictor colli facialis mentralis in *Eurystomus* 281
constrictor colli spinalis in Chelonia .. 262
Ophidia 267
constrictor colli spinalis profundus in Chelonia 263
constrictor pharyngei in *Amblystoma* .. 174
Anura 184
Axolotl 158
Coecilia 190
Molge 179
Myxophyes tadpoles 147, 148, 151
Necturus 165
Neoceratodus 141
coraco-branchialis in Chondrostei .. 53
Holocephali 57
Neoceratodus 142
coraco-hyo-glossus in *Molge* 179
coraco-mandibularis in *Neoceratodus* 142
cranio-hyoideus in Anura 184
Myxophyes tadpoles .. 149, 151
csd.2 in *Dromaeus* 277
Eurystomus 281
Struthio 277
csv.1 in *Eurystomus* 279
csv.1*a*. *See* submentalis.
in *Dromaeus* 275
Struthio 275
csv.1*b*. *See* intermandibularis.
in *Dromaeus* 275
Struthio 275
csv.2 in *Dromaeus* 277
Gallus 274
Struthio 277
csv.2*a* and 2*b*. *See* superficial ventral hyoid constrictor.
cucullaris in *Amblystoma* 173
Anura 186
Axolotl 160
Neoceratodus 141
Molge 179
Myxophyes tadpoles .. 147, 149

PAGE
Muscles—*continued.*
deep branchial constrictor in Batoidei 38
Chondrostei 53
Heterodontus 28
Selachii 12
Teleostei 64
deep hyoid constrictor in Batoidei .. 41
Chondrostei 54
Heterodontus 31
Selachii 16
deep mandibular constrictor in Batoidei 43
Crocodilia 258
depressor labii superioris brevis in *Myxophyes* tadpole .. 145, 150
depressor labii superioris longus in *Myxophyes* tadpole 145, 148, 150
depressor mandibulae, phylogenetic history 168
in *Amblystoma* 172
Anolis 247
Anura 182
Axolotl 157
Basiliscus 248
Chelonia 262
Coecilia 189
Crocodilia 258
Diemyctylus 177
Dromaeus 277
Eurystomus 281
Gallus 274
Geckos 251
Molge 178
Myxophyes tadpole 145, 149
Necturus 163
Ophidia 268
Plethodon 177
Psittaci 285
Physignathus 244
Sphenodon 254
Struthio 277
depressor mandibulae mandibularis in *Physignathus* 240
depressor mandibulae superioris in Holocephali 59
depressor palpebrae inferioris in *Physignathus* 238
depressor rostri et veli in Holocephali 57
dilator hyoidei in *Myxophyes* tadpole 144, 148, 150
dilator laryngis in Coecilia 190
dilator operculi in Teleostei 81
dorsal mandibular constrictor in Holocephali 59
dorso-laryngeus in *Amblystoma* .. 174
Anura 185
Axolotl 158
Coecilia 190
Myxophyes tadpole 149, 151
epiarcualis rectus in Teleostei .. 67
epiarcualis transversus in Teleostei .. 67
epibranchial spinal in Batoidei .. 39
Heterodontus 29
Selachii 13
Teleostei 64, 66
erector of the barblets in Siluridae 182
genio-abdominis in Coecilia 191
genio-glossus in *Amblystoma* 175
Anura 186
Axolotl 160
Chameleon 250
Chelonia 263

PAGE
Muscles—*continued.*
  Crocodilia 259
  Myxophyes tadpole 149
  Ophidia 268
  Physignathus 246
 genio-hyo-coracoideus in *Molge* .. 179
 genio-hyoideus in *Amblystoma* .. 175
  Anura 185
  Chameleon 250
  Chelonia 263
  Coecilia 191
  Dromaeus 278
  Myxophyes tadpole .. 147, 149, 151
  Neoceratodus 142
  Ophidia 268
  Physignathus 246
  Struthio 278
  Teleostei 70
 genio-hyoideus inferior et superior in Teleostei 72
 hypobranchial in the Axolotl 159
  Myxophyes tadpole 146, 151
  Neoceratodus 141
 hypobranchial spinal in Axolotl .. 159
  Batoidei 46
  Chondrostei 53
  Heterodontus 28
  Neoceratodus 142
  Ophidia 268
  Selachii 13
  Teleostei 70
 hyoglossus in *Amblystoma* 175
  Anura 186
  Chameleon 250
  Chelonia 263
  Crocodilia 259
  Eurystomus 282
  Myxophyes tadpole 151
  Ophidia 268
  Physignathus 246
 hyoglossus anterior in *Amblystoma* .. 175
  Gallus 274
 hyoglossus posterior in *Gallus* .. 274
 hyohyoideus in Teleostei 77
 hyohyoideus inferior in Teleostei .. 72
 hyohyoideus superficialis in Teleostei 72
 hyohyoideus superior in Teleostei .. 72
 hyoid in Aves 286
  Dromaeus 277
  Eurystomus 281
  Gallus 272
  Struthio 277
 hyoid adductor in Batoidei 41
  Heterodontus 32
  Teleostei 70
 hyoid depressor in Batoidei 70
 hyoid levator in Batoidei 41
  Heterodontus 31
  Selachii 18
 hyomandibularis in *Chameleon* .. 250
  Chelonia 264
  Crocodilia 259
  Dromaeus 278
  Eurystoma 282
  Gallus 274
  Physignathus 246
  Struthio 278
 hyopharyngus internus in Coecilia .. 190
 hypobranchial in Theria .. 306–309
 infrabasibranchialis in Teleostei .. 69

PAGE
Muscles—*continued.*
 infraspinatus in Axolotl 160
  Myxophyes tadpole 149
 interarcualis dorsalis in Teleostei .. 67
 interbranchialis in *Amblystoma* .. 173
  Axolotl 158
  Holocephali 57
  Necturus 165
  Neoceratodus 140
 interbranchialis 4 in Coecilia .. 191
 interceratohyoideus in *Eurystomus* .. 282
  Gallus 274
 interhyoideus in *Amblystoma* 173
  Anura 181
  Axolotl 157
  Chameleon 249
  Chelonia 262
  Chondrostei 54
  Coecilia 189
  Crocodilia 257
  Diemyctylus 177
  Dromaeus 277
  Eurystomus 281
  Gallus 274
  Gekkonidae 251
  Holocephali 59
  Molge 178
  Myxophyes tadpole 144, 148
  Necturus 164
  Plethodon 177
  Sphenodon 253
  Struthio 277
 intermandibularis in *Amblystoma* .. 172
  Anolis 247
  Anura 180
  Axolotl 155
  Chelonia 260
  Chondrostei 54
  Coecilia 188
  Crocodilia 255
  Diemyctylus 176
  Eurystomus 280
  Gekkonidae 250
  Molge 177
  Myxophyes tadpole .. 143, 148, 149
  Necturus 161
  Ophidia 265
  Physignathus 238
  Teleostei 76
  Plethodon 176
  Varanus 252
 intermandibularis posterior in Teleostei 70
 laryngeal in *Amblystoma* 196
  Amphiuma 195
  Hyla 199
  Ichthyophis 198
  Molge 196
  Myxophyes tadpole 194
  Necturus 195
  Spelerpes 179
 laryngeus ventralis in Coecilia .. 190
 latissimus dorsi in Axolotl 160
 levator arcus palatini in Teleostei .. 80
 levator hyoidei in Coecilia 189
  Myxophyes tadpole .. 146, 148, 151
  Necturus 163
 levator hyomandibulae in Chondrostei 54
 levator labii inferioris in *Callorhynchus* 60
 levator maxillae superioris in *Amia* .. 81
  Chondrostei 55
 levator operculi in Chondrostei .. 54

PAGE
Muscles—*continued.*
  Holocephali 59
  Teleostei 79
 levator quadratri in Coecilia .. 188
  Dromaeus 277
  Psittaci 285
  Phalacrocorax 283
  Struthio 277
 levator scapulae inferior in Anura .. 186
 levator scapulae superior in Anura .. 186
 marginales in Axolotl 158
  Neoceratodus 140
 mandibular in *Dromaeus* 275
  Gallus 270
  Ophidia, synonymy of 266
  Physignathus 241
  Eurystomus 279
  Struthio 275
  Selachii, serial homology of 47
  Theria 304–306
 mandibular adductor in Batoidei .. 44
  Heterodontus 33
  Selachii 21, 25
  Teleostei 82
 mandibular constrictor in Selachii .. 19
  Teleostei 70
 mandibular epiarcual oblique in
   Batoidei 43
  Selachii 22
 mandibular levator in Selachii .. 21
 masseter in *Dromaeus* 275
  Gallus 270
  Psittaci 284
  Struthio 275
 masseter major in Anura 184
  Ophidia 266
 masseter minima in Anura 184
 masseter minor in Anura 184
  Ophidia 266
 massetericus in Coecilia 188
  Eurystomus 280
  Myxophyes tadpoles 146, 148, 151
  Ophidia 266
  Phalacrocorax 283
  Podargus 279
 middle hyoid adductor in Chondrostei 54
 obliquus dorsalis in Teleostei .. 67
 omo-abdomino-hyoideus in *Amblystoma* 175
 omo-hyoideus in Anura 187
  Chameleon 250
  Myxophyes tadpole 148
 petro-hyoideus anterior in Anura .. 184
 pharyngo-hyoideus in Teleostei .. 69
 posterior digastric in Theria .. 303
 protractor hyoidei in Teleostei 72, 76
 protractor labii superioris in Holocephali 60
 protractor maxillae in Siluridae .. 81
 pterygo-quadratus in *Varanus* .. 252
 pterygoideus in Anura 183
  Axolotl 155
  Batoidei 43
  Chondrostei 55
  Coecilia 188
  Holocephali 60
  Molge 177
  Myxophyes tadpole 145, 151
  Necturus 162
  Neoceratodus 136
  Selachii 22
  Spelerpes 179
  Teleostei 86

PAGE
Muscles—*continued.*
 pterygoideus anterior in Crocodilia .. 256
  Ophidia 267
 pterygoideus externus in Chelonia .. 260
  Crocodilia 256
  Dromaeus 277
  Eurystomus 280
  Gallus 271
  Ophidia 266
  Physignathus 246
  Podargus 279
  Psittaci 284
  Struthio 277
 pterygoideus inferior in Crocodilia .. 256
 pterygoideus internus in Chelonia .. 261
  Coecilia 188
  Crocodilia 256
  Dromaeus 277
  Eurystomus 281
  Gallus 272
  Phalacrocorax 283
  Physignathus 240
  Podargus 279
  Psittaci 285
  Ophidia 267
  Sphenodon 255
  Struthio 277
 pterygoideus medius in Chelonia .. 261
  Crocodilia 256
  Dromaeus 277
  Eurystomus 280
  Gallus 271
  Ophidia 269
  Phalacrocorax 283
  Physignathus 240
  Psittaci 285
  Struthio 277
 pterygoideus posterior in Psittaci .. 247
 pterygo-quadratus in *Anolis* .. 247
  Physignathus 241
 quadrato-abdominis in *Myxophyes*
   tadpole 147, 149
 quadrato-mandibularis in Axolotl .. 156
  Batoidei 44
  Chondrostei 55
  Dromaeus 276
  Eurystomus 180
  Gallus 271
  Heterodontus 35
  Holocephali 60
  Neoceratodus 136
  Phalacrocorax 283
  Psittaci 284
  Selachii 24
  Spelerpes 180
  Struthio 276
 retractor anguli oris in Crocodilia .. 255
  Ophidia 266
  Physignathus 239
  Sphenodon 254
  Varanus 252
 retractor dorsalis arcuum branchialium
   in Teleostei 66
 retractor labii superioris in *Drepane* .. 82
 rhomdoideus anterior in Anura .. 186
 spheno-pterygoideus in *Dromaeus* .. 277
  Gallus 272
  Ophidia 267
  Phalacrocorax 283
  Podargus 279
  Physignathus 241
  Psittaci 285

Muscles—*continued.* PAGE
Struthio 277
Varanus 252
spheno-pterygoideus anterior. *See* Corrigenda.
spheno-quadratus in *Eurystomus* .. 281
sphincter laryngei in *Myxophyes* tadpole 151
sterno-hyoideus in *Eurystomus* .. 283
sterno-mandibularis in Crocodilia .. 259
sterno-thyroideus in Chelonia .. 264
Eurystomus 283
sterno-thyroideus lateralis in *Physignathus* 245
sterno-thyroideus medialis in *Chameleon* 249
Crocodilia 259
Physignathus 245
sterno-thyroideus profundus in *Chameleon* 249
Physignathus 246
stylohyoideus in Theria 302
subarcualis obliquus in Axolotl .. 159
Chondrostei 53
Teleostei 68
subarcualis rectus in Axolotl .. 159
Coecilia 190
Myxophyes tadpoles 146, 148, 151
Necturus 164
Neoceratodus 142
Teleostei 68
subarcualis transversus in *Myxophyes* tadpole 146, 148, 151
Neoceratodus 141
Teleostei 68
subhyoideus in *Myxophyes* tadpole.. 149
submentalis in *Anolis*.. 247
Anura 180
Amblystoma 172
Axolotl 155
Basiliscus 247
Chelonia 260
Coecilia 188
Crocodilia 255
Diemyctylus 176
Eurystomus 279
Molge 177
Myxophyes tadpole .. 143, 148, 149
Necturus 161
Ophidia 264
Physignathus 239
Plethodon 176
Spelerpes 179
Sphenodon 253
Teleostei 70
Tiliqua 251
Varanus 252
superficial branchial constrictor in Axolotl 158
Batoidei 37
Chondrostei 53
Heterodontus 28
Selachii 11
Teleostei 64
superficial dorsal branchial constrictor in *Necturus* 165
superficial facial in Theria .. 297–302
superficial facialis constrictor in *Gallus* 273
superficial hyoid constrictor in Batoidei 39
Chondrostei 54
Heterodontus 31
Holocephali 59

Muscles—*continued.* PAGE
Physignathus 244
Selachii 14
superficial mandibular constrictor in Batoidei 43
Heterodontus 33
Neoceratodus 134
superficial ventral hyoid constrictor in Amphibia, synonymy of .. 169
Axolotl 153
Chelonia 261
Coecilia 189
Crocodilia 257
Diemyctylus 176
Molge 178
Necturus 163
Ophidia 267
Plethodon 179
Spelerpes 179
superficial ventral mandibular constrictor in Holocephali 59
temporalis in Anura 183
Axolotl 155
Chelonia 260
Dromaeus 276
Eurystomus 280
Gallus 270
Molge 177
Myxophyes tadpole .. 145, 148, 151
Necturus 161
Ophidia 266
Phalacrocorax 283
Podargus 279
Psittaci 284
Spelerpes 180
Struthio 276
temporomasseterícus in Crocodilia 255
Physignathus 239
Teleostei 84
thoracico-hyoideus in Coecilia .. 191
thyro-glossus in Crocodilia 259
thyro-hyoideus in *Chameleon* .. 250
Chelonia 263
Dromaeus 278
Eurystomus 282
Gallus 274
Physignathus 246
Struthio 278
thyro-mandibularis in *Chameleon* .. 250
Physignathus 246
thyro-pharyngeus in Crocodilia .. 259
trapezius in Anura 186
Batoidei 46
ventral constrictor in *Gallus* 270

N

Necturus, synonymy of branchial muscles 164
Nerve abducens, a transported part of motor vii 93
facial, in *Dromaeus* 277
Eurystomus 281
Gallus 272
Struthio 277
patheticus, a transported part of motor v 93
v in Coecilia 188
Eurystomus 281
Molge 178
v and vii in Axolotl 156
Neoceratodus 139
Physignathus 243
ix and x in *Gallus* 273

PAGE

Neuronomeres and their motor and sensory nerves, table of 93

Notophthalmus 177

Nomenclature adopted 9

P

Palatine bone in fishes 126

Paradicichthys, skull of 105

Pars cephalognathica. *See* Muscle depressor mandibulae in Amphibia and Sauria.

Pars netognathica. *See* Muscle depressor mandibulae in Amphibia and Sauria.

Phylogeny of Amphibia .. 218–229
  evidence of cephalic muscles 230–232
  fishes 218

Platycephalus, skull of 104

Polypterus, lower jaw of 118, 120

Primitive bony fish, skulls of 114

Pseudotriton 179

R

Rana, metamorphosis of muscles .. 153

S

PAGE

Sauramphibia 216–218
Scomber, lower jaw of 120
Selachian muscles, table of 11
Selachii, most primitive living fish .. 92
Skull of *Amia* 113
  Anura 205–207
  Archaic fishes 203
  Bony Fishes 104
  Carcharius arenarius 94
  Chondrostei 100
  Coecilia 118–211
  Dipnoi 200–205
  Embolomeri 213–216
  Euamphibia 205–212
  Heterodontus 97
  Lepidosteus 116
  Polypterus 118
  Primitive Bony Fish 114
  Stegocephalians 211–212
  Urodela 208–209
  Urolophus 97
Superior maxillary bones, evolution of.. 122

T

Teeth of fishes 121

U

Urolophus, skull of 97

S1932